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SOIL-BORNE FUNGI AND THE CONTROL OF ROOT DISEASE

by

S. D. GARRETT

(Rothamsted Experimental Station)

Price, 2s. 6d.

(Published by the Imperial Bureau of Soil Science, Harpenden, England)

1939

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Soil-borne Fungi and the Control of Root Disease

1. INTRODUCTION

The study of plant diseases caused by soil-borne fungi has in recent years been approached in a new way. Such problems were formerly under the care of general plant pathologists, engaged in investigating a variety of pathological conditions in the crops under their charge. The soil was not unnaturally regarded as an additional technical complication incidental to research on the subterranean activities of a root-infecting fungus. Attempts were made to eliminate the complexities of the soil environment by the establishment of pure culture conditions, and by the use of highly artificial methods of inducing disease. With increasing facilities for specialization in plant pathology, however, workers were able to devote their whole time to the study of soil-borne diseases, and often to those of a single crop. This undoubtedly led more rapidly to the realization that the pure culture method of experimentation with the root-infecting fungi was far from satisfactory when the time arrived for applying experimental results to field practice. Plant pathologists were thus forced into a closer study of the soil environment in which the root-infecting fungi lived. Particularly important was the fuller realization by mycologists that these pathogenic fungi were not occupying a purely physico-chemical habitat, but one teeming with an active and most diverse population of micro-organisms, of which the plant pathogens formed numerically a comparatively negligible minority. Similar conclusions were voiced by Fawcett (1931) in a general warning to plant pathologists on the dangers of following too exclusively the pure culture methods in the study of disease initiated by Koch, and on the importance of supplementing them by working with associations of micro-organisms, and by studies under more natural conditions.

There is now probably no need to emphasize the conclusion that further advances in the study of this group of plant diseases will best be made, if not by team work, at least by soil scientists viewing the soil as an integral whole rather than by plant pathologists regarding it as an obstacle to investigation. The importance, again, of viewing the soil as a dynamic biological equilibrium can hardly be over-emphasized. In this connection, particular credit should be given to the earlier work of the Canadian group of investigators (Sanford, 1926; Simmonds, 1928a; Sanford and Broadfoot, 1931; Henry, 1931-32; Broadfoot 1933a and b) on the role of microbiological antagonism in the natural control of soil-borne fungus diseases of plants. The value of the soil microbiological approach to these problems of plant pathology was forecast by Sanford (1933a).

A logical approach to the problem of controlling a soil-borne disease is by way of a preliminary geographical and edaphic survey of its occurrence. It is likely that, under certain soil conditions, a natural control of the disease will be found to occur. Scientific investigation is as likely to achieve successful control by the elucidation and extension of a naturally occurring control as by the discovery of anything absolutely new. Indeed, "new" control methods arising out of such work are frequently found to represent merely a return to agricultural practices formerly prevalent, but since abandoned owing to pressure of economic circumstances, or to other considerations. The soil environment is fortunately more within the control of the farmer or grower than the subaerial environment, and a considerable degree of modification can be effected by soil and crop management. At the same time, it seems likely that the future may see an increase in an alternative method of disease control, whereby the production of a particular crop is limited to soil types unfavourable to dangerous root disease.

The rapidly increasing output of published work on soil-borne fungus diseases during the last few years is held now to justify some review of the progress achieved in their control. A classification of commonly employed control methods will be put forward, when it will be seen that although certain basic principles of control are common to the soil-borne fungus diseases of all crops, yet the diseases of intensive crops, of annual and biennial field crops, and of plantation crops all have their own particular control methods. A classification of control methods is therefore suggested as follows :—

(i) Production of disease-resistant varieties of the crop plant.
(ii) Plant sanitation.
(iii) Elimination of infectious material from the soil.
(iv) Adjustment of soil conditions to check activity of parasite.
(v) Augmentation of host resistance.

The use of a variety of crop plant, in which resistance to disease has been combined with other desirable qualities by the processes of selection and hybridization, is, of course, the ideal control method for the grower of the crop. Apart from the technical difficulties of combining disease resistance with good yielding capacity and high quality of product, however, it is sometimes idle even to look for disease-resistant varieties. Such are generally to be found only when the pathogenic fungus is restricted to a single species of host plant, or to a number of closely related species or genera of plants. At the same time, there is no doubt that breeding for disease resistance has proved one of the most widespread and successful methods of control for soil-borne fungus diseases. Where the method can be employed, it is generally completely effective, and the first cost is the only one. Few plant pathologists would dispute an assertion that this control method and that of seed treatment by fungicides probably save the agricultural industry of the world more money than all the other control methods for soil-borne fungus diseases put together. But since neither

of these important methods of control employed against the soil-borne fungus diseases is directly concerned with the soil itself, but belongs rather to the domains of plant genetics and of general plant pathology, respectively, it is not proposed to give them more than incidental mention in this review.

The remaining control methods will be considered in their natural order. Thus it seems logical to consider methods of plant sanitation, whereby the introduction of infectious material into the soil may be avoided, before the application of methods designed to eliminate such material once it has become part of the soil. Yet elimination of fungus inoculum before or during the growth of the crop will generally involve less disturbance of normal cropping routine than will adjustment of soil conditions under the growing crop so as to inhibit or impede the activity of the parasite. In conclusion will be considered those control methods in quite another class, whereby a soil-borne disease is checked or even eliminated altogether by changing the growing conditions of the crop in such a way as to increase resistance to infection. Some diseases might really be more correctly ascribed to faulty physico-chemical conditions of the soil or subaerial environment, which when once corrected leave the plant no longer susceptible to infection by the parasite organism or organisms.

2. THE ROLE OF FUNGI IN THE SOIL

The important part played by fungi in the decomposition of the soil organic matter is by now thoroughly established (Waksman, 1931 ; Brierley, 1923 ; Russell, 1937). The soil fungi are especially concerned with the decomposition of plant roots and of other crop residues on and in the soil. The tissues of the higher plant constitute a freshly-exposed habitat which is colonized by a micro-ecological succession of soil fungi with which are associated, more especially in the latter stages, other members of the soil microflora and microfauna. Under normal conditions, the plant tissues become available for colonization by the soil micro-organisms at or shortly before the natural death of the plant, or of certain parts of the plant. In the case of disease, however, the roots and other underground parts of the plant may be colonized by parasitic organisms when still living and in full vigour.

At one time it was generally considered that many of the soil fungi causing plant disease might be able to persist indefinitely in the soil, in the absence of their appropriate hosts, by living on the soil organic matter. A few of these fungi, such as *Plasmodiophora brassicae*, the agent of club-root of crucifers, and *Synchytrium endobioticum* causing wart disease of potatoes, were indeed found to be *obligate parasites*, non-cultivable upon any known culture medium, and as such had eventually to die out in the soil in the continued absence of appropriate host plants. But the great majority of the parasitic forms were found to be *facultative saprophytes*, which could be cultured without difficulty upon the usual laboratory media, and generally grew well enough upon sterilized soil.

Experience with a variety of soil-borne fungus diseases such as pink-root of onions (Hansen, 1929) and take-all of wheat (Garrett, 1936), has, however, shown that the primary parasite which opens up the root habitat is rapidly followed by a succession of other fungi and soil micro-organisms. The sequence of micro-organisms in the infected roots of strawberry and tobacco seedlings has been studied by means of a direct microscopical technique developed by Hildebrand (1934), Koch (1935) and Hildebrand and Koch (1936). The next stage of colonization after that by the primary parasite may be made by a regularly occurring secondary parasite, for example, *Fusarium malli* after *Phoma terrestris* in pink-root of onions (Hansen, 1929) and *Fusarium culmorum* after *Ophiobolus graminis* in take-all of wheat (Garrett, unpublished).

It now seems probable, therefore, that the majority of the more highly specialized root-infecting fungi are confined, as regards active existence, to the living roots or other underground parts of their host plants, and are unable to compete for food material with the secondary parasites and saprophytes developing in the infected plant tissues. The true obligate parasites, of the *Plasmodiophora brassicae* type, and the semi-obligate parasites, of the *Ophiobolus graminis* type, are thus restricted to the first stage in the colonization of the host-plant tissues. But there are also, on the other hand, root-infecting fungi of a less specialized type which can undeniably exist in the soil both as parasites and as saprophytes. Such a one is *Fusarium culmorum*, which has been recorded as a wound parasite of such a variety of cultivated plants as asparagus, aster, sugar-beet, chrysanthemum, hyacinth, pea, potato, rice, tobacco and tomato. It is best known, however, as causing a seedling blight of cereals (Simmonds, 1928b ; Blair, 1937) and a foot-rot condition of the older plants (Bennett, 1928), and is also commonly found as a wound parasite following upon primary infection of wheat and barley by *Ophiobolus graminis*. Very recently, Sadasivan (in press) has found that *F. culmorum* plays an important part, as a saprophyte, in the early decomposition of healthy wheat straw buried in the soil.

The species of *Rosellinia* may be cited as a more familiar example, especially to observers in tropical countries, of this type of unspecialized parasite-*cum*-saprophyte. A rapid growth through dead leaves or other surface litter, particularly in damp and shady situations, constitutes the well-known habit of this widely distributed genus. At the same time, *Rosellinia* can behave as a dangerous though incidental parasite to the stems and roots of tea bushes (Tunstall, 1922 ; Petch, 1928 ; Gadd, 1937) and other plantation crops (Nowell, 1923) with which it comes into contact in the course of its growth through the surface litter.

It thus appears that the soil fungi can be ecologically grouped according to their relation in time to the decomposition of plant remains. The obligate and semi-obligate parasites are confined to the initial stages of decomposition, whilst certain less specialized parasites can continue to live saprophytically on the killed tissues. Certain saprophytes, on the

other hand, are found only in the later stages of decomposition of the plant residues. The conclusions of Thom and Morrow (1937) are so pertinent in this connection as to merit quotation, "Soil fungi may possibly be divided into two sections; (1) those capable of living normally in relation to soil organic matter in the chemical sense, i.e., to residual products of decomposition; and (2) those concerned in primary decomposition, i.e. the breakdown of plant and animal remains towards those residual products."

Our present conceptions of the varied relations between soil fungi and higher plants owe much to the extensive researches of Reinking and Manns (1933-34) and of Reinking (1934-35) on the soil *Fusaria* of tropical America. As the result of a very large series of isolations from soils, these authors concluded that the tropical American soil *Fusaria* could be divided into two groups, *soil inhabitants* and *soil invaders*. The *soil inhabitants* were those species of *Fusarium* found in all, or nearly all, of the soils examined, and were hence regarded as common soil saprophytes. Certain other species, on the other hand, were found to have a local distribution only, and this distribution was further found to coincide with the presence, or past presence, of the appropriate host plant. With the death of the host plant, the numbers of such a species gradually dwindled, until it disappeared from the soil, and was hence designated as a *soil invader*.

These conclusions of Reinking and Manns have been adopted elsewhere by Garrett (1938b) as a basis for the ecological classification of the root-infecting fungi. "The *soil inhabitants* are considered to be primitive or unspecialized parasites with a wide host range; these fungi are distributed throughout the soil, and their parasitism appears to be incidental to their saprophytic existence as members of the general soil microflora. The *soil invaders*, to which class the majority of the root-infecting fungi seem to belong, are more highly specialized parasites; the presence of such fungi in the soil is generally closely associated with that of their host plants. In the continued absence of a host plant, such fungi die out in the soil, owing to their inability to compete with the soil saprophytes for an existence on non-living organic matter. This close association between the *soil invaders* and their host plants thus seems to be enforced by the competition of the general soil microflora."

These later developments in our knowledge of the ecology of the soil fungi are really an extension of Waksman's (1917) postulate that there is a definite fungus flora of the soil. From his examination of the fungi found in 25 different soils collected from widely separated regions of the North American continent, and from the Hawaiian Islands, and from the results of European investigators, Waksman concluded that the basic fungus flora of the soil was essentially cosmopolitan, though the relative importance of different groups might vary with latitude and soil type. Thus soils of the northern latitudes were characterised by abundance of *Mucorales* and *Penicillia*, whilst *Aspergilli* were predominant in the warmer soils. Again, the genus *Trichoderma* was found especially in acid soils

(e.g. forest soils) and in waterlogged soils. The conception of a basic fungus flora of *soil inhabitants*, amongst which might be found exotic fungi or *soil invaders*, thus really originated with Waksman (1917), and due acknowledgment of this fact is indeed made by Reinking and Manns (1933).

Other aspects of the relation between soil micro-organisms and the roots of plants are discussed in a review by Loehwing (1937), which embraces the whole of this important field of ecology.

3. PLANT SANITATION

The general principles of plant sanitation are common to the control of all soil-borne diseases, without exception, but the precise mode of their application varies with almost every individual disease. The aims of plant sanitation are twofold, firstly to prevent infectious material in the shape of diseased crop residues from being turned into the soil, and secondly to prevent the dispersal of the pathogenic organism by various agencies to fresh areas.

(A) Disposal of Infected Material

The amount of infectious material to be turned into the soil after harvesting an annual field crop could, of course, be greatly reduced by the periodical rogueing of obviously diseased plants throughout the growing season of the crop. Such rogueing is rarely economically practicable, however, so that the problem is therefore how to dispose of such diseased crop residues as are left above ground after harvest. This is most commonly done by burning the diseased material *in situ*, a method which has been practised for many years in Australia for control of the take-all disease of wheat (McAlpine, 1902, Griffiths, 1933). Wheat is harvested there with the "stripper," which removes the heads alone, leaving the long straw standing. The standing straw never fails to burn well after the hot dry summer, and there is a complete destruction of the basal infected parts of the stubble. Although the infected roots of the wheat plants are still left in the soil, these are less resistant of decomposition than is the above ground part of the stubble, so that the amount of diseased material surviving in the soil for infection of the next crop of wheat is substantially reduced by the burn. This practice of firing the straw assists also in the control of another soil-borne parasite of the wheat crop, viz *Urocystis tritici*, causing the flag smut disease (McAlpine, 1910). The burning, or carting off the land, of crop residues cannot, however, be very strongly recommended for the control of disease, since it is likely to lead to serious depletion in the humus content of the soil. This results on the one hand in a tendency to soil erosion, and on the other in impoverishment of microbiological activity and soil fertility. Since a high level of microbiological activity is now known to exert a strong natural check on the pathogenic fungi, it is apparent that the burning of crop residues may be bad policy even from the point of view of the plant pathologist alone.

The disposal of infected material by the grower of a plantation crop presents other difficulties. The cost of digging out is generally an appre-

ciable item, whilst the material has usually to be carted off in sacks and burnt elsewhere. These considerations led Smith (1931-32a) to evolve a method of treating *in situ* the infected stumps of Panama-diseased banana plants. After cutting down the main stem and suckers to within 6 inches of the soil, heavy gas oil is poured onto the cut surfaces, which absorb it, and into the surrounding soil. The stump is thus killed, and no adventitious growth can be put out.

(B) Preventing Dispersal of the Fungus

The dispersal of a fungus from an original focus of infection can occur in a variety of ways. Specialized dispersal forms, such as air-borne conidia, may be responsible. Survival organs such as resting spores and sclerotia may prove more effective in dispersal, however, owing to their much greater longevity and powers of resistance to unfavourable conditions. Dispersal of the fungus in the form of infected plant material is perhaps the most important way in which soil-borne diseases are spread to new areas. The scattering of diseased crop residues can be brought about by a variety of natural agencies, but of greater importance is the distribution of disease by the planting-out in clean soil of diseased seed, seedlings, suckers or cuttings, and perennating organs, such as bulbs, corms and tubers.

Dispersal by planting operations

A variety of plant diseases are carried by the true seed, either mechanically as spores adhering to the seed coat, or held within the glumes or bracts, or as a latent mycelial infection. The former type of infection can be controlled by dressing the seed with a protective fungicide before sowing. Since many important diseases of plants are carried over in this way from one crop to the next, this cheap and exceedingly effective method of control must be reckoned as one of the most outstanding practical achievements of plant pathology in preventing loss due to disease. Bunt of wheat (*Tilletia tritici* and *T. laevis*) is now rarely to be seen in the fields of good farmers in agriculturally progressive countries. Whilst many farmers still dress their own seed, co-operative seed treatment is increasing, and treated seed is now often supplied by the seedsman. Control of a latent mycelial infection, which cannot be reached by a surface fungicide, is more difficult. The "modified hot-water treatment" invented by Jensen (1888), is still used for control of loose smut of wheat (*Ustilago tritici*) and of barley (*U. nuda*), but is not widely employed, on account of the difficulties of operation, which involve careful supervision, and also because the treatment is liable to result in germination injury to the seed. An ingenious application of this principle of control has been worked out by Luthra and Sattar (1934) for Indian conditions. The treatment is carried out in June or July; the infected seed is pre-soaked in water at indoor temperature for 4 hours from 8 a.m. to 12 noon, and is then taken out and exposed to the sun from 12 noon to 4 p.m. Complete control of loose smut infection has been obtained in this way, and the reduction in germination of the treated seed is negligible (not exceeding 2 per cent). The

method is said to be applicable only to the hotter parts of the Punjab plains; maximum shade and sun temperatures at Lyallpur in June are stated to be 49° and 55°C. (120° and 131°F), respectively. Good reviews of the principles and practice of seed treatment are given by Martin (1936) and by Leukel (1936). Another way in which a fungus may be disseminated with plant seed is in the form of sclerotia mixed up with the seed, e.g. the sclerotia of *Sclerotinia trifoliorum* may not infrequently be found in clover seed, whilst the "ergots" of *Claviceps purpurea* may occur in threshed grain of rye and other cereals.

A fungus may also be carried over on the perennating organs used for propagation, such as bulbs, corms, and tubers. Thus the majority of the important fungus diseases of the potato may be carried over on and in the tuber, e.g. wart (*Synchytrium endobioticum*), scab (*Actinomyces scabies*), stem canker (*Rhizoctonia solani*), wilt (*Verticillium albo-atrum*, *Fusarium oxysporum* and *F. solani* var. *eumartii*), and blight (*Phytophthora infestans*), as well as most of the bacterial and virus diseases of this plant. The spread of disease by means of infected cuttings and by other methods of vegetative propagation is too general for citation of individual examples. Spread of disease by means of seedlings transplanted from an infected seed-bed is another common way in which a fungus may be rapidly distributed over large areas of healthy land.

Dispersal by wind

Wind dispersal of infected plant debris is commonly quoted as a source of infection of new land, and of re-infection of clean soil, though few experiments have been performed to determine the rapidity or extent of spread of infected material in this way. Wind-borne fragments of infected wheat straw and dry grass haulms carrying the fungus were considered by McAlpine (1902) to be responsible for the spread of the take-all disease (*Ophiobolus graminis*) of wheat in Australia, and later field observations by Samuel (1924) supported this suggestion. Crawford (1934) cites the blowing of loose dry soils in dust storms as one method of spread of the *Fusarium annuum* wilt of chilli peppers in New Mexico.

Wind dispersal of root-infecting fungi by means of their conidia or other air-borne spore forms is a question requiring critical investigation for individual disease organisms. The mere formation and aerial dispersal of such spores cannot be taken as proof of their efficiency as agents of infection. As an eminent example of this argument *de forma* may be quoted the hypothesis of air-borne spore infection of jungle stumps considered by Bryce (1922), Petch (1928), and others to explain outbreaks of root rot in young plantations of tea, rubber, cacao and other tropical crops planted on the site of the felled jungle. These authors suggested that the cut surfaces of the jungle tree stumps were infected by air-borne spores of the parasites, which grew thence into the roots of the stumps. No critical experiments in support of the hypothesis have been published, however, and it has not been accepted either by Napper (1932a) or by Briton-Jones

(1934). The observations and experiments of Napper (1932a, 1932b-37) suggest that infection by the root parasites is distributed underground here and there throughout the original jungle, but in such a natural mixed association, the parasites are in equilibrium with their hosts, and nowhere is infection very apparent. The clearing of this mixed association and its replacement by a uniformly susceptible population, in the shape of the young rubber plantation, affords greater opportunity for the spread and destructive activity of the rubber root parasites. Napper therefore considers that root disease trouble in young rubber plantations represents merely a development from sources of infection already present on the roots of the original jungle, perhaps roused into greater activity by the operations of felling and burning in clearing the jungle. Gadd (1936-37), however, has observed that almost 100 per cent of *Grevillea* shade trees on certain tea estates in Ceylon, known to be perfectly healthy before felling, have become infected as stumps by such fungi as *Fomes noxius* and *Ustulina zonata*; infection contracted after felling by the stumps then passes to the tea, and lines of dying tea bushes are to be seen marking out the underground lie of the *Grevillea* stump roots. Since *Ustulina zonata* is a well-known wound parasite, generally gaining entrance through broken limbs and pruning cuts, Gadd's assumption that infection of the *Grevillea* stumps (indisputably healthy *before* felling) took place via the exposed cut surface is a reasonable one.

Fomes noxius, however, is apparently more frequently associated with this type of infection in Ceylon than is *Ustulina zonata*, according to Gadd, and evidence is lacking that this fungus is at all a frequent colonizer of cut wood surfaces. The importance of microbiological antagonism in the colonization of exposed wood surfaces by air-borne fungi is indeed recognised by Gadd (1936), whilst Napper (1934) has shown that *Fomes lignosus* cannot infect injured roots already colonized by a wound parasite such as *Ustulina zonata*. An alternative mode of infection of the cut stumps, *via the roots*, is suggested by the observations of Wallace (1935) in Tanganyika, and of R. Leach (1937) in Nyasaland. These authors observed that whilst *Armillaria mellea* normally occurred to a comparatively slight extent on the jungle roots, the operation of felling apparently lowered the resistance of the roots of the stumps to such an extent that *A. mellea* was eventually to be found in the stump of almost every individual member of certain susceptible species of tree, such as *Parinarium mobola, having gained entrance via the roots*. This possibility has therefore to be taken into account when considering the observations of Gadd (1936-37), and a similar one by Kalis (1938), who found development of red root rot (*Ganoderma pseudoferreum*) to follow the felling of *Albizzia* shade trees on tea estates in West Java.

No proof of the infection of uninjured tree roots by spores of any species of the Basidiomycetes, or "higher fungi," is available. This is, indeed, considered to be doubtfully possible by Tunstall (1930), De Jong (1933), and Gadd (1936), who quote observations and experiments to show

that infection of tree roots by these fungi apparently fails to occur in the absence of an adequate nutritive substrate behind the infection hyphae. Gadd (1936) has further made the highly significant suggestion that this need of the infecting hyphae for a *food base* is probably the factor limiting the spread of infection by many fungi to root contact. He argues that only those fungi which can use the soil humus as a food base, e.g. the species of *Rosellinia*, are able to escape this restriction. Sharples (1936), speculating upon the origin and evolution of the rhizomorphous habit, suggests that the tropical root disease fungi are developing their subterranean habit at the expense of their former powers of aerial spread. Thus he remarks (p. 181): "In Malaya, the rhizomorphs of *F. lignosus* and *G. pseudoferreum* obviously provide an efficient means of vegetative propagation. Therefore the production of fructifications and spores may be considered a laborious process in these two cases, and the formation of rhizomorphs provides a special means of short circuiting the slow development of the fructifications." And again (p. 185): "Methods of vegetative propagation, when effective, generally tend to replace methods of sexual reproduction necessitating the production of elaborate fructifications and spores."

Another example of the argument from design is provided by the suggestion of Samuel and Garrett (1933) that the coincidence of severe outbreaks of the take-all disease of wheat in South Australia with seasons of high spring rainfall was to be explained by ascospore dispersal of the fungus over the wheat paddocks, in showery weather. Proof that actual spore dispersal could so occur was provided for the first time by these authors, but increasing knowledge of the subterranean spread of *Ophiobolus graminis* has rendered an alternative theory of the epidemiology of this disease increasingly probable. Garrett (1939) has finally shown that the ascospores of this fungus are capable of infecting the roots of wheat seedlings growing in bacteriologically sterile soil or sand, but not those in unsterilized or partially sterilized soil. It is therefore improbable that ascospore infection of wheat roots can occur in the field, so that these spores are probably to be regarded as a non-functional relic of a less specialised ancestral form of *O. graminis*.

All attempts, again, to produce infection by the conidia of *Phymatotrichum omnivorum*, the cotton root rot fungus, have apparently failed, and Taubenhaus and Ezekiel (1931) conclude from their field observations that other evidence for spore dissemination of this fungus is lacking. These observations are quoted to show that the mere production, and even the effective dispersal, of aerial spores by a root-infecting fungus does not constitute proof, or even establish an *a priori* case, that such spores are agents of infection in the field. The production of these apparently non-functional spore forms is to be taken as a sign of evolution, since they are characteristic, on the whole, of the more specialized fungi.

Dispersal by water

The contamination of glasshouse water supplies by the spores of parasitic fungi was investigated by Bewley and Buddin (1921), who found

surface water such as that from ponds and brooks to be much more heavily contaminated than Company's water or that from deep artesian wells. Curzi (1927) found that *Phytophthora hydrophila*, causing foot rot of chilli peppers in Italy, was spread by water ; a single irrigation was said sometimes to result in the complete destruction of the crop. For the control of a similar disease (here attributed to *P. palmivora* var. *piperis*) of chillies in Batavia, Muller (1936) recommended that a network of shallow trenches should be dug, with water pits at intervals to prevent the rain-water running off over the surface. If infection occurred in one of the squares isolated by the trenches, the soil and diseased plants were to be watered with a one per cent solution of copper sulphate, and weeding temporarily discontinued. Crawford (1934) has commented upon the spread by irrigation water of the *Fusarium annuum* wilt of the same crop in New Mexico. Thung (1932) found *Phytophthora nicotianae*, the agent of black shank of tobacco in Java, to be carried by water from old tobacco fields, manure heaps, and curing barns. The movement of water in erosion and drainage from infected upper levels was considered by King *et al.* (1934b) to result in the infection of lowlands and deltas by *Phymatotrichum omnivorum*. Peltier (1937) repeatedly observed that when root rot occurred near the headwaters of a stream, it was usually distributed throughout the drainage basin, and that the incidence of the disease increased at the lower levels. A similar observation on the spread of *Armillaria mellen* has been made by Hewitt (1934). The dispersal of sclerotia of *Sclerotinia sclerotiorum* by irrigation and flood water has been noted by Brown and Butler (1936) in their study of lettuce " drop " in Arizona. The importance of the passive spread of pathogenic fungi by water movement has thus been well established. Active spread by free-swimming zoospores of Phycomycetes and other " Lower Fungi " is probably of negligible importance as far as actual dispersal is concerned. For instance, Haenseler (1926) found that zoospores of *Aphanomyces euteiches* were apparently incapable of migrating even half an inch in the soil, so that practically no spread of the disease in this way occurred under his experimental conditions.

Dispersal by cultivation operations and farm movements

Infected soil may be carried on the feet of farm labourers, and on those of draught animals and stock, as well as on implements. Such methods of spread have been cited, for example, by Gibbs (1931) for the spores of *Plasmodiophora brassicae* on New Zealand farms, and by Brown and Butler (1936) for the sclerotia of *Sclerotinia sclerotiorum* in Arizona.

Dispersal by feeding diseased plant material to stock

The feeding of diseased roots to stock is considered by Gibbs (1931) to constitute another mode of dispersal of *Plasmodiophora brassicae*, whilst Brown (1937) found *Sclerotinia sclerotiorum* to be spread in Arizona by feeding farm animals on infected lettuce refuse. On the other hand, sheep and other stock could be made to further the ends of plant sanitation by folding them on the infected plants after harvest, and quarantining the

animals for four days, the maximum period for evacuation of living sclerotia. McAlpine (1910) condemned the practice of feeding farm horses on wheat hay infected with flag smut (*Urocystis tritici*), and Clayton (1925) has attributed the rapid spread of the disease in New South Wales to neglect of precaution against this possibility, having shown that viable spores of *U. tritici* are voided in horse-dung.

Dispersal by insects and the soil fauna

The relation of insects to the spread of plant diseases has been reviewed by Leach (1935); this relationship is probably more important in the case of bacterial plant pathogens, which are often not only transmitted, but also introduced into the host tissues by insect agency. The majority of plant-parasitic bacteria are apparently incapable of direct penetration of the uninjured host organs, and are hence more dependent upon plant injury by insects, etc. Some interesting experiments are reported by *Taubenhaus and Christenson* (1936), who were able to recover *Fusarium vasinfectum*, the agent of cotton wilt, from the faecal pellets of caged insects or larvae fed on tissues of wilt-infected cotton plants. The cultures of this fungus thus isolated were proved to be pathogenic to cotton plants, but the fungus did not survive passage through wireworms, Collembola, and Japygidae. Leach and Dosdall (1938) have demonstrated that viable spores of *Alternaria* and other fungi are commonly disseminated in the infrabuccal pellets of ants. Dealing with a very different type of vector, Gleisberg (1922) found the infectivity of *Plasmodiophora*-infected soil to be somewhat increased by passage through earthworms, whilst Fedorintchik (1935) has confirmed the observation that the fungus can be so transmitted in a viable condition.

Dispersal by manures and composts.

These agencies are frequently cited as responsible for infection of clean soil, but it is possible to over-estimate their importance in this connection. If we except the common soil-inhabiting fungi that are to be classed as incidental parasites (p. 9), there are probably very few parasitic fungi that can spread actively in the manure yard or compost heap. Moreover, since the processes of decomposition, given favourable conditions, are generally more rapid in the heap than in the soil, the mycelium and less resistant resting forms of parasitic fungi will generally have been decomposed by the time that the manure is ready for use.

4 ELIMINATION OF INFECTIOUS MATERIAL FROM THE SOIL

Pathogenic fungi survive in the soil in the absence of suitable host plants in a variety of ways, viz :—

(i) As growing vegetative mycelium. This mode of survival applies only to facultative parasites or true soil inhabitants, such as the *Rosellinia* spp. Life is maintained on vegetational refuse as a

substrate ; *Rosellinia* spp. are thereby enabled not only to survive indefinitely in the absence of living hosts, but also to spread about in the soil.

(ii) As thin-walled conidia, or other dispersal spore forms.

(iii) As resting spores, with thick and biochemically-differentiated enclosing walls.

(iv) As sclerotia, or aggregates of resting mycelium, frequently showing differentiation of an outer layer of more resistant cells.

(v) As resting mycelium in infected plant residues.

Conditions governing the survival of pathogenic fungi in the soil have been discussed elsewhere (Garrett, 1938b), so it is proposed to consider here rather the application of research findings to practice, in the evolution of methods of eradicating such fungi from the soil. Such control methods, when assembled together, fall into well-marked groups, which are associated with different types of crop production, viz :—

(a) *By fungicides and by heat*—methods applied chiefly in the cultivation of intensive glasshouse and market garden crops, and for the control of disease in seed-beds generally.

(b) *By mechanical methods*—digging-out, and rogueing. Such methods are applied chiefly in the cultivation of plantation crops.

(c) *By crop rotation* } methods designed for the grower
(d) *By biological control* } of annual and biennial field crops.

(A) Fungicides and Heat Treatment

These methods are of chief importance in the sanitation of the seed-bed, and in the intensive cultivation of glasshouse and market-garden crops. Under such conditions, effective crop rotation is generally impossible, and the use of the soil is not infrequently restricted to the raising of a single crop. The continuous growth of a single species of crop plant soon leads to a falling-off in yields. Under a system of crop rotation, the variable demands of different crops upon the mineral resources of the soil tend to cancel one another out, whereas under single cropping, a lack of balance in the fertilizer resources of the soil more quickly results. The effect of root excretions was at one time considered to play a part in leading to an " unhealthy " state of the soil under single cropping, but the influence of this factor is now generally discounted (Loehwing, 1937). Undoubtedly more important, however, is the building-up of a high population of the parasites and pests appropriate to the particular crop under continuous cultivation. A combination of these effects leads, sooner or later under the continuous cropping system, to a state of " soil sickness." This can occur under field conditions, and has been investigated in wheat by Bolley (1913), in flax by Bolley and Manns (1932), in strawberries by Hildebrand (1934), in tobacco by Koch (1935), and in raspberries by Berkeley (1936). The onset of " soil sickness " is not generally mitigated by the application of

fertilizers, and indeed the excessive and uncontrolled application of fertilizers to glasshouse crops may intensify the condition, for which it may sometimes even be mainly responsible. This type of trouble, brought on by enormous dressings of dung and artificial fertilizers and by very heavy surface waterings, may be remedied according to Bewley (1934) by incorporation of raw straw in vertical walls in the soil during the making up of the beds. The roots seek out these areas of good aeration and drainage, and make excellent growth, whilst the straw facilitates the entry of water into the soil.

It was independently discovered by Girard (1894) in France and by Oberlin (1894) in Alsace that " partial sterilization " of the soil by carbon disulphide remedied the condition of soil sickness. Other volatile antiseptics were found to have the same effect, and the discovery by Darbishire and Russell (1907) that heat could be similarly employed soon followed. A history of the work on partial sterilization of the soil is given by Russell (1937) and by Waksman (1931), together with a discussion of the various hypotheses put forward to account for the beneficial effects produced, of which the control of noxious pests and plant-disease organisms constitutes only a part.

Partial sterilization of the soil has therefore become a regular routine in the intensive cultivation of glasshouse crops. It is not proposed to enter here into practical details of methods of heat treatments employed, or to catalogue the various types of organic and inorganic fungicides in use for this purpose in glasshouse, seed-bed, and field. Excellent and well-documented accounts of soil treatment by heat and by fungicides are given in the textbooks of Martin (1936) and of Cunningham (1935). Those interested in partial sterilization of the soil by steam, dry heat, electricity, and chemicals should read also the papers by Hartley (1921), Hunt *et al.* (1925), Wiant (1929), Bewley (1931), Newhall *et al.* (1931), Newhall and Nixon (1936), Kadow and Anderson (1937), and Ezekiel (1938a and b), as a selection from the very extensive literature accumulating upon the subject.

An efficient soil fungicide must be reasonably cheap. In the second place, it must be able to penetrate to that depth of soil from which reinfection of the new crop can occur. The cause of poor penetration is generally adsorption by the colloidal particles of the soil. Formaldehyde was shown by Hunt *et al.* (1925) to be particularly efficient in this respect, in as much as its penetration equalled that of the water carrying it in solution. Thirdly, the fungicide must be decomposed in the soil with reasonable celerity, otherwise residual toxicity will damage the next crop and impair the fertility of the soil. It is sometimes argued that the use of fungicides for the control of plant pathogenic organisms is a bludgeoning method destroying beneficial and harmful organisms alike. Such an objection can reasonably be lodged against the use of inorganic salts of mercury and copper as soil fungicides. Residual toxicity of such compounds to the crop following can be observed and appreciated, where it is sufficiently

obvious. A more insidious danger is that the continued and uncontrolled use of such chemicals will, if unchecked, cause an accumulation of mercury or copper in the soil sufficient to check microbiological activity, and hence to impair soil fertility. The employment of decomposable antiseptics, such as the coal-tar derivatives, may on the other hand be expected eventually to increase soil fertility. The work of Buddin (1914) and of Matthews (1924) showed that the application of such compounds as carbon disulphide, benzene, toluene, and naphthalene, whilst at first exerting a partial-sterilization effect, eventually resulted in a very large rise in bacterial numbers, which Matthews showed to be proportional to the heat of combustion, and hence to the energy value, of the antiseptic. The addition of energy materials to the soil may eventually result in an increased fixation of atmospheric nitrogen, owing to stimulation of the nitrogen-fixing bacteria (Waksman, 1931).

The chief difficulties in the way of effective use of partial sterilization by heat and by soil fungicides are as follows :—

(i) The subsoil acts as a reservoir of infection which is tapped by the roots of the first crop grown in the treated soil. The pathogenic fungus travels up inside or outside the infected root (see p. 35) to the treated surface soil, which may soon become thoroughly reinfected. The occurrence of such re-infection from the subsoil seriously impairs the efficiency of steam sterilization for the control of *Verticillium cinerescens* wilt of the perpetual flowering carnation, according to Wickens (1935), and many growers are now using raised beds effectively insulated from the subsoil, by means of drain tiles, bricks, or cement, in order to obviate such reinfection. Frequently, too, reinfection of sterilized soil in pots occurs from roots growing down through the drainage hole in the bottom of the pot into contaminated soil or cinders on which the pots are standing.

(ii) The danger of such reinfection is enhanced by the fact that parasitic fungi spread much more quickly, whether through the soil or over the roots of the host plant, in completely or partially sterilized soil than in unsterilized soil. This may be attributed both to increase in available food material liberated by sterilization of the soil organic matter, which may often increase vigour of infection and rate of spread by the parasite, and to removal of microbiological competition, which normally acts as a strong check on the activity of pathogenic fungi in unsterilized soils (see p. 26 *et seq.*). Attention was early drawn to this danger by Hartley (1921), who suggested re-inoculation of the partially sterilized soil with a mixture of saprophytic micro-organisms, before use in the seed-bed.

(iii) Soil fungicides cannot reach mycelium of a parasite lying dormant in bulky or resistant plant residues buried in the soil. Thus Tunstall (1926) observed that no chemical treatment would ever obviate the necessity for complete eradication of old tea roots, harbouring root-disease fungi, from the soil. Chemical treatments may, however, be used in combination with buried root extraction as an additional safeguard in the preparation of fresh planting sites (see also p. 22 and p. 36).

These various difficulties incidental to effective soil sterilization by heat or by fungicides are sometimes avoided by the practice, almost confined to glasshouse growers, of replacing " sick " or " worn-out " soil with " healthy " soil not previously used for intensive production of the particular crop or crops for which it is intended. Sterilization of a compost may, in the same way, be avoided by the preparation of a new compost from fresh ingredients. This practice is really the inverse of crop rotation, inasmuch as it is the soil and not the crop which is changed ; the overhead expenses of glasshouse cultivation severely restrict the grower's choice of crops, and make effective crop rotation impossible.

(B) Mechanical Methods

These methods, comprising digging and rogueing, are used chiefly in the control of soil-borne fungus diseases of plantation crops. Their maximum development has been attained only in the tropics, thanks to a plentiful supply of cheap labour. The root diseases of tropical plantation crops are almost always a legacy from the original jungle. The jungle trees, growing in a natural mixed association, have attained an equilibrium with their root parasites, and nowhere is the effect of parasitism very apparent. This must be attributed to the inability of a parasitic fungus to spread rapidly or extensively along the root network underground in a population containing only a proportion of susceptible host species. When the jungle is cleared, however, the activity of the parasites appears to be stimulated (Napper, 1932a). The observations of Wallace (1935) and of Leach (1937) upon *Armillaria mellea* in Tanganyika and Nyasaland, respectively, have shown that the proportion of individuals parasitized by this fungus in the untouched jungle may be very small ; the operation of felling, however, appears sharply to lower the resistance of the roots to infection, so that subsequently the stumps of almost every individual tree of certain susceptible species, such as *Parinarium mobola*, are found to be thoroughly infected by this fungus. Observations and experiments along these lines on other of the tropical root disease fungi are lacking at present (p. 13), but it seems likely that this phenomenon may be comparatively general.

If a uniform population in the shape of young trees of the future plantation crop—be it rubber, tea or other tropical crop—is now planted over the cleared area, any fungus root parasite able to infect the young trees will find ideal conditions for survival and spread. The laying down of the cleared area for a few years to annual field crops, e.g., maize millet, sorghum, or to sugar cane, etc., not susceptible to the jungle root-disease fungi, would eliminate much of the infectious material surviving on the jungle roots. This solution of the problem is undoubtedly effective (Napper, 1932a, Gadd, 1936), but does not appear to have been generally acceptable in the past. The method of " clean clearing " has accordingly been generally adopted in the preparation of a felled and roughly cleared jungle site for the reception of a young plantation crop. By this method,

the soil of the entire plantation area is dug through to a depth of six inches to one foot by native labour, and all the larger pieces of root carefully removed, whether they are obviously infected or not.

An entirely new method of dealing with root disease in young rubber plantations has been worked out by Napper (1932-38), depending upon the principle of periodical rogueing. From an examination of field experiments conducted at the Rubber Research Institute of Malaya, Napper (1932a) concluded that clean clearing as a preparation for young rubber was less satisfactory than formerly supposed. Absolutely clean clearing, in which all buried infected material was removed from the soil, would certainly ensure a healthy plantation of young rubber. But rubber planted after ordinary " clean clearing," in which the smaller pieces of infected root were left in the soil, suffered more from root infection in the first three years of the experiment than did rubber planted on an uncleared site :—

Table I

Percentage infection in young rubber planted on jungle site

(Napper 1932a)

	Cleared	Uncleared	Secondary jungle (belukar)
Block 1	29.4	18.6	—
,, 2	20.3	9.2	—
,, 3	—	—	1.7

When secondary jungle, or " belukar," was allowed to grow up amongst the young rubber, the percentage of infected rubber trees was least of all. Napper explains these results as follows. It appears that *Fomes lignosus* does not begin to form its rhizomorphs until the food supply in the infected root has been exhausted, and until the latter has been reduced, in fact, to a mere shell. The larger pieces of infected timber will therefore not be dangerous to the young rubber roots for some time, i.e. until the food reserves have been exhausted and rhizomorph formation starts. The small pieces of infected root, however, such as are left in the soil after ordinary clean clearing, quickly reach the stage of rhizomorph formation and become dangerous. Now the rhizomorphs of *Fomes lignosus* are apparently unable to spread for any appreciable distance through the soil alone, like the rhizomorphs and runner hyphae of many other root-infecting fungi (Garrett, 1938b), and prefer living roots along which to spread. Other solid surfaces will apparently do almost as well, but only living roots can furnish a new food supply to the *Fomes* rhizomorphs, as this fungus is sensitive to the antagonism of other micro-organisms, and will not enter dead or wounded roots already colonized by wound parasites such as *Ustulina zonata* and saprophytes. When the land is left uncleared, therefore, the rhizomorphs arising from the smaller pieces of infected root are offered other solid surfaces as well as the roots of the young rubber trees upon which to spread, and their energy is dissipated into a maze of tributaries. When young secondary jungle (belukar) is allowed to grow up, the effect is, of course, enhanced. This diversion

of the *Fomes* rhizomorphs into numbers of small tributaries growing along the maze of smaller roots is believed by Napper to constitute the protective effect exercised by the belukar upon the roots of the young rubber trees.

A new method for the eradication of root disease in young rubber areas, which is applicable not only to *F. lignosus*, but also to *Ganoderma pseudoferreum* and *F. noxius*, has accordingly been worked out, and practical details are given in a recent publication by Napper (1938). The ground, after felling and burning of the jungle, is cleared of the larger stumps, but the young rubber trees are themselves employed for the discovery of residual sources of infection, as follows. Every 4 to 6 months, a pest gang of trained labourers makes a tree-to-tree inspection of the whole plantation, in the course of which the upper taproot and laterals of every young tree are examined for rhizomorphs of the root-disease fungi. The length of taproot which must be exposed varies from 2 inches at one year after planting to 9 inches at four years, if the soil is a deep one, but the depth of inspection must in any case be sufficient to uncover the undersides of the surface laterals. If rhizomorphs of a root disease fungus are found, the root system is opened up further until the whole extent of the invading mycelium has been exposed, and the source of infection discovered. The source of infection is then removed (and destroyed) and the roots of the jungle stumps are followed up systematically in every direction until all infected material has been disclosed and removed. The root system of the young rubber tree is then pruned of all root sections which have already been penetrated by the parasite. The method depends for much of its success upon the fact that the rhizomorphs of *F. lignosus*, the most common cause of root disease, extend for 5-15 feet ahead of the infected part of the root. The roots carrying such superficial or epiphytic mycelium can be disinfected simply by pulling away the larger rhizomorphic strands, and then washing the root surface with a 2 per cent solution of copper sulphate. Napper states that this epiphytic habit of the *F. lignosus* rhizomorphs renders it possible, by this periodical treatment, to bring a stand of young rubber through a heavy attack of *F. lignosus* without losing more than 20 per cent of the trees which have become infected. The rhizomorphs of the other two members of the Malayan root-disease complex, *G. pseudoferreum* and *F. noxius*, are epiphytic only for some 18 inches in advance of penetration, so that a proportionately greater loss of trees infected by these two fungi is inevitable. Owing to the fact that these fungi occur sparsely by comparison with *F. lignosus*, however, the efficiency of the control method is not seriously impaired. In this way, root disease can be eliminated before the roots of the trees have expanded into their full planting sites (after some 5 years); once the roots of neighbouring trees begin to interlace, spread of infection becomes, of course, at once more rapid and more dangerous.

The method of rogueing has here been employed as an alternative to clean clearing for the eradication of infected material from the site of a plantation crop. In other cases, the main purpose of the rogueing method

is the prevention of centrifugal spread of a root disease (see p. 36, *et seq.*). Another new and quite different method of eliminating root disease from the site of a plantation crop has been developed by Leach (1937) (p. 34).

(C) Crop Rotation

This is one of the oldest methods of controlling soil-borne diseases, and is dependent upon specialization of parasitism in the pathogenic organisms. Its value becomes restricted with increase in host range of the parasite, so that the control of such a fungus as *Phymatotrichum omnivorum*, with a known host range of more than 1,700 species (Streets, 1937), by crop rotation severely curtails the range of possible crops which can safely be grown. Fortunately, however, this fungus cannot attack monocotyledons (Ezekiel and Fudge, 1938) so that a rotation of cotton with maize, sorghum and small grains can be followed. A wide host range not only diminishes the number of possible rotation crops, but also increases the number of weed hosts, or " ground keepers," which can carry the parasite, again a problem with *P. omnivorum* (Taubenhaus, 1936).

Control by crop rotation may be unsatisfactory for reasons other than the wide host range of the parasite, or the difficulty of effectively excluding weed hosts from the rotation. The resting spores of some of these soil parasites are long-lived; for example, Schaffnit (1922) reported that potatoes contracted wart disease, due to *Synchytrium endobioticum*, on plots that had been kept fallow and free of weeds for 10 years. The survival of a fungus in sclerotial form may similarly impede control by crop rotation. Taubenhaus and Ezekiel (1936), in a laboratory test, obtained a 10-15 per cent survival in sclerotia of *Phymatotrichum omnivorum* after these had been kept in a clay soil for 5 years. Conditions of burial, viz, in closed containers, would have been relatively unfavourable to factors making for loss of viability, in this test. Rogers (1936) invented a machine for separating the sclerotia of *P. omnivorum* from soil samples; with the aid of this machine, which could handle as much as four tons of soil per day, he studied (1937) the effect of different crop rotations upon the population of viable *P. omnivorum* sclerotia in the soil, in relation to the percentage of root-rot infection in the cotton test crop. A 3-year rotation of cotton with two crops non-susceptible to the fungus reduced neither the percentage of root rot nor the population of viable *P. omnivorum* sclerotia. A 4-year rotation, involving three years under non-susceptible crops, constantly reduced disease by about 100 per cent. The sampling for sclerotia was done on a large scale, 320 samples being taken per acre at 1, 2 and 3 foot depths with a 6-inch post-hole auger, and 9 acres under different rotations or continuous cotton were surveyed each year. The type of rise and decline in sclerotial population occurring in each successive year of the 4-year rotation may be illustrated by data taken from Rogers's (1937) paper (p. 679).

Table 2

Number and viability of *Phymatotrichum omnivorum* sclerotia in a 4-year rotation as related to time interval since last planting of cotton (after Rogers, 1937)

Time interval	No. of sclerotia	No. of viable sclerotia	Per cent viable sclerotia
End of cotton year	4488	1665	37.1
End of first year under non-susceptible crop	9201	5765	62.7
End of second year under non-susceptible crop	2681	1479	55.2
End of third year under non-susceptible crop	1617	560	34.6
Continuous cotton	10,500	6959	66.3

One feature of particular interest in these data is the fact that the highest sclerotial population, and the greatest percentage viability of sclerotia in that population, occur not at the end of the cotton season, but at the end of the first year under a non-susceptible crop. This finding is in excellent agreement with the general conception of sclerotia as organs formed by a fungus with decreasing vegetative activity of the mycelium, which may or may not be brought about by exhaustion of the substrate. In this respect, sclerotial formation by *P. omnivorum* must be considered analogous to rhizomorph production by *Fomes lignosus* (Napper, 1932a).

The size of sclerotia may determine to some extent their term of viability ; those of *P. omnivorum* range in size, according to Rogers (1937), from less than 1 mm. to more than 1 cm. in diameter. A similar study to that of Rogers was carried out by Leach and Davey (1938) upon survival under different rotations of the considerably smaller sclerotia of *Sclerotium rolfsii*, which average 1.2-2.5 mm. in diameter, according to these authors. Good correlation was obtained between numbers of viable sclerotia per square foot of soil, and percentage infection of the host crop, sugar beet. The figures of Leach and Davey show a comparatively rapid decline in population of viable sclerotia under a crop non-susceptible to this fungus, numbers being commonly reduced to one third or one quarter of the original population in an interval of 6 months, whilst in one case numbers were reduced from 4810 in December to 150 (viable sclerotia per sq. foot of soil) in the following July.

The disappearance of sclerotia may result both from their germination and dissipation as mycelium, and from their decomposition by the other soil micro-organisms. More information is indeed required concerning factors governing sclerotial germination in the soil ; in the meantime, we may conclude that whilst the formation of sclerotia by a fungus at the conclusion of its period of parasitic activity may necessitate the employment of a longer rotation, it does not necessarily invalidate rotation as a means of control.

Other cases are on record where the data at present available do not permit us to assign the longevity of a fungus either to carrier hosts, or to long-lived resting spores or sclerotia. For example, Barker (1923) reported that it was frequently impossible to grow flax varieties susceptible to wilt

(*Fusarium lini*) more than once every 10-12 years on the same land, whilst Melhus *et al.* (1926) found the cabbage yellows organism, *F. conglutinans*, to last for at least 11 years in the soil ; a survival period of 14 years under grass was previously reported by Jones and Gilman (1915) for the same fungus, which was responsible for a severe outbreak of yellows in the first cabbage crop planted on the ploughed-up sod. H. T. Cook (1937) has reported that *Fusarium bulbigenum* var. *niveum*, causing water-melon wilt, can persist for 16 years in the soil in the absence of the host crop. It is thus difficult to resist the conclusion that these wilt-producing *Fusaria* can live as saprophytes on the soil organic matter, and should thus provisionally be classed in the group designated by Reinking and Manns (1933) as *soil inhabitants*, or true soil fungi, as distinct from the group of *soil invaders*. The observation of Cook (1937) on *F. bulbigenum* var. *niveum*, cited above, agrees with Reinking and Manns's classification of *F. bulbigenum* as a true *soil inhabitant* of the tropical American soils which formed the subject of their classical study.

Crop rotation as a method of control is therefore less efficient in the case of those fungi capable of living to any appreciable extent as saprophytes on decomposing plant remains. The recent discovery by Sadasivan (in press), that *Fusarium culmorum*, well-known as a parasite of cereals and other plants, plays an important part in the early decomposition of normal wheat straw when buried in the soil, suggests that this fungus is probably ineradicable from the soil by ordinary crop rotation, though it may be thereby kept within bounds.

(D) Biological Control

The growing promise of biological control as a practical agricultural method has engaged the attention of an increasing number of workers on the soil-borne fungus diseases of plants. Biological control is nothing new, and its operation has always constituted a valuable natural check upon the activities of the root-infecting fungi and of other soil-borne pathogens. It is therefore with increasing the operation of this salutary factor rather than with its introduction that present research work is concerned.

The antagonism of micro-organisms on culture media and in the host plant has been observed for many years, but it was not until more recently that the full significance of this phenomenon has been appreciated by soil mycologists. Machacek (1928) published an important paper on the association of phytopathogens in the host and on culture media, whilst this field was subsequently reviewed by Fawcett (1931). The field of biological antagonism, with special reference to the cereal foot-rot fungi, was later covered by Garrett (1934), whilst associative and antagonistic effects of micro-organisms in general have been recently summarized by Waksman (1937). Porter and Carter (1938) and Weindling (1938) have discussed very fully the physiological interactions of fungi with fungi and with other micro-organisms on culture media, in soil, and in the host plant,

whilst Garrard and Lochhead (1938) have exhaustively reviewed those aspects of microbiological antagonism which concern the soil-borne diseases of plants and their control. Since these different reviewers have given the history of the earlier and more fundamental papers on this subject, there is no need to do so here.

The principles of biological control are simply stated. The soil population is a dynamic biological equilibrium. The continued growing of a particular crop encourages the multiplication of the root parasites of that crop (Bolley, 1913); the application of an organic manure encourages the multiplication of the saprophytic organisms engaging in the successive stages of its decomposition. Since the encouragement of one group generally occurs at the expense of others, it has been reasonably assumed on *a priori* grounds that the incorporation of organic manures in the soil, by encouraging the development of saprophytes, will check the activity of the plant parasites. This check may operate in several ways, (i) the assimilation, respiration and excretion of the saprophytes may check that of the parasites, (ii) the saprophytes may actually attack and assimilate the mycelium, etc., of the parasites. These two effects may be distinguished as *fungistatic* (or growth-inhibiting) and *fungicidal*, respectively, and both have been demonstrated in the biological control of *Ophiobolus graminis* (p. 28). It will be appreciated that the method of biological control, like that of crop rotation, will be most effective against those organisms which have become highly specialized to a parasitic life, i.e., the *soil invaders*.

The method of biological control is thus essentially an ecological one, inasmuch as changes are induced in the constitution of the soil population by appropriate soil treatments—chiefly the application of organic manures. Certain investigators (van Luijk, 1938) have suggested that biological control of plant parasites may be obtained by suitable inoculation of the soil with specific micro-organisms selected for their "antagonistic ability," or by addition of their growth products. The micro-organisms, however, have generally been isolated from the soil in the first place. Insufficient attention has been paid, moreover, to Broadfoot's (1933b) finding that antagonism of a saprophyte to a plant pathogenic fungus on a selected culture medium was not a reliable indication that it would exert any degree of control upon the parasite in the soil. Deficiencies in the soil population of mico-organisms can rarely be the factor limiting biological control under natural conditions, and no inoculation of the soil, however heavy, with such a selected "antagonist" as *Trichoderma lignorum* can have more than a transient effect in changing the microbiological balance of the soil population, as Weindling and Fawcett (1936) have correctly concluded from their valuable experiments on the control of *Rhizoctonia solani* damping-off of citrus seedlings by *T. lignorum* (p. 32).

An important exception to this general rule is to be found under the highly artificial conditions of sterilized soil, which are very favourable to the spread of re-introduced parasites, both through the liberation of food material by sterilization of the soil organic matter, and by the elimination

of normal microbiological competition (p. 19). One of the first investigators to demonstrate this unwelcome effect of heat sterilization of soil was Hartley (1921), who showed that *Pythium de Baryanum* was more active in "damping-off" pine seedlings in pots of sterilized soil than in the same soil simultaneously re-inoculated with saprophytic micro-organisms. He suggested that heat-sterilized soil should therefore be so reinoculated with saprophytes before being used for the raising of seedlings. The treatment of heat-sterilized soil in such a way as to hasten its return to normal is a practical problem for soil microbiologists; some form of re-inoculation with "healthy" unsterilized soil, and subsequently incubation under optimum conditions, is obviously required.

Control of potato scab (*Actinomyces scabies*) by green manuring with grass cuttings was first reported by Millard (1921). Sanford (1926) suggested that such control was brought about through the antagonism to *A. scabies* of saprophytic species of bacteria developing on the decomposing green manure (rye grass). Further experiments by Millard and Taylor (1927) showed that the development of scab on potatoes grown in sterilized soil inoculated with *A. scabies* could be reduced by simultaneous inoculation of the soil with *A. praecox*, an obligate saprophyte of much more vigorous vegetative growth. By increasing the proportion of *A. praecox* to *A. scabies* in the inoculum, the degree of scabbing on the test potatoes was reduced from 100 per cent to nil. The sterilized soil evidently provided sufficient food material for a good development of *A. praecox*, and only a rather small increase of control was given by the admixture of grass cuttings, sterilized along with the soil. Millard and Taylor concluded that, whilst their tests were concerned only with the biological control of *A. scabies* by *A. praecox*, it was likely that soil bacteria might exercise a similar controlling effect, as suggested by Sanford (1926). The recent experiments of Goss (1937) have convincingly demonstrated the controlling effect of the general soil microflora upon the development of scab (p. 30), though he failed to secure any result with an inoculation of *A. praecox* alone. Environmental conditions can completely reverse the reaction of one organism upon another, however, as elegantly demonstrated by Rosen and Shaw (1929) with *Sclerotium rolfsii* and *Fusarium vasinfectum*; on acid media of pH less than 6.9, *S. rolfsii* grew over *F. vasinfectum*, whereas if the pH of the medium was 7.0 or over, the reverse occurred.

Further attention was drawn to the possibilities of biological control by the experiments of Canadian workers with the cereal foot-rot fungi. For the purpose of making pot and field experiments with one of these fungi, it was customary to culture the organism upon some organic medium, such as cooked wheat kernels, a mixture of oats and pearl barley, oat hulls, or a mixture of soil or sand with cornmeal, etc. The infected material was buried in the experimental soil, often in rather large quantities. Such inoculum did not prove very satisfactory, however, owing to its rapid deterioration in virulence; after a few months, inoculated soils often proved completely harmless to cereal seedling plants therein. Since this

deterioration was more rapid in field soil than in sterilized or partially sterilized soil in pots, Simmonds (1928a) suggested that it was due to the operation of microbiological antagonism upon the pathogenic inoculum. The truth of this suggestion was largely established by the experiments of Sanford and Broadfoot (1931), who found that infection of wheat seedlings by *Ophiobolus graminis* was completely suppressed by the antagonistic action of a number of fungi and bacteria, not only by the living cultures, but also, in many cases, by their culture filtrates as well. Henry (1931) found that the growth of *Helminthosporium sativum* upon sterilized soil in small flasks might be completely suppressed by the addition of very small amounts of unsterilized soil, or by simultaneous inoculation with a number of other fungi and bacteria, so that no infection resulted when wheat seeds were inoculated with the contents of the flasks in small pots. Broadfoot (1933a) showed that infection of wheat seedlings by *Ophiobolus graminis*, initially much less in unsterilized than in sterilized soil, fell off markedly with the progress of recolonization of the sterilized soil by the returning microflora. Moritz (1932) observed that the severity of the *Ophiobolus* disease of wheat on three German soils could be inversely correlated with the "protective" action of the general soil microflora, which was estimated by comparing infection in the unsterilized soil with that obtained in the sterilized soil. The interaction of microbiological antagonism with temperature was first demonstrated by Henry (1932) for wheat seedling infection by *Ophiobolus graminis*. Henry's findings were confirmed by Garrett (1934), and extended to other cereal foot-rot fungi. Rising soil temperature was found by these authors to increase microbiological antagonism to the parasitic fungus ; the true effect of high soil temperature in accelerating infection could be seen under sterile conditions, but, in the presence of other soil micro-organisms, was masked by their inactivation of the pathogen inoculum, which increased with rising temperature.

Field control of the take-all (*Ophiobolus graminis*) disease of wheat in Kansas by the application of such organic materials as chicken and horse manure, alfalfa stems and leaves, boiled oats and barley, and potato flour, was very briefly reported by Fellows (1929). The possibilities of organic manuring for the control of this disease have been further investigated by Garrett (1936-38a). Evidence was presented (1936-37) to show that the factor chiefly controlling the subterranean spread of this fungus along the roots of the wheat plant was the accumulation of carbon dioxide, with corresponding lowering of the oxygen tension, in the microclimate of the root zone. The concentration of carbon dioxide, to which this fungus is especially sensitive, is controlled by the relative rates of (i) its formation by combined respiration of the infected root and rhizosphere zone of accelerated microbiological activity (Starkey, 1929-38) and (ii) its diffusion away from the root zone. The rate of diffusion depends both upon the physical and chemical nature of the soil (i.e. soil texture and reaction), and upon the difference in concentration of carbon dioxide at the source and at the sink of diffusion. For the diffusion of this gas from the root towards

a sink of zero concentration in the surrounding soil (e.g. as in freshly sterilized soil) will obviously be more rapid than diffusion towards a sink of one per cent concentration. For this reason, therefore, a high rate of soil respiration checks the growth of *Ophiobolus* along the wheat root by increasing the local concentration of carbon dioxide, not only directly, but also indirectly by retarding its diffusion away from the root. Maintaining soil respiration at a sufficient level by periodical organic manuring will thus help to control the subterranean activity of *Ophiobolus* on the roots of the growing wheat crop ; most effective, in this respect, however, is the preparation of a firm, well compacted seed-bed for the wheat crop (p. 40).

Biological control of the *parasitic phase* of *Ophiobolus* is thus considered to be chiefly *fungistatic* (or growth inhibiting). The operation of biological control on the *resting phase* of this fungus, on the other hand, appears to be truly *fungicidal*. Thus in its resting phase as mycelium inside infected wheat stubble buried in the soil (Garrett, 1938a), *Ophiobolus* was found to tolerate adverse physical conditions of the soil better than those optimum for microbiological activity. For example, decline in viability was indefinitely postponed in air-dry soil and in soil at 2° — 3°C., and was less rapid in a waterlogged soil than in one maintained at medium moisture content. Loss of viability was hastened, on the other hand, by treatments promoting increased general microbiological activity in the soil, such as partial sterilization followed by reinoculation, or improvement in soil aeration. Most effective in this respect proved to be the addition of organic materials poor or lacking in nitrogen, such as rye-grass meal, wheat straw or starch, to the soil. The effectiveness of the organic matter fell off with increasing nitrogen content, and organic materials with a nitrogen content considerably in excess of their requirements for complete decomposition were found to be ineffective, and, indeed, might even delay the disappearance of *Ophiobolus*. The same result was obtained by supplementing an effective material (glucose) by increasing additions of nitrogen as ammonium carbonate. These observations led to the hypothesis that the mycelium of *Ophiobolus* is assimilated as a source of nitrogen by the micro-organisms engaged in the decomposition of the matrical wheat straw. The number of attacking micro-organisms and the general nitrogen scarcity are increased by the addition to the surrounding soil of organic materials poor or lacking in nitrogen. On the other hand, the addition of organic substances rich in nitrogen, such as dried blood, or of inorganic nitrogen as ammonium carbonate, is considered to protect the *Ophiobolus* mycelium by offering a more readily available source of nitrogen for decomposition of the matrical cereal straw. It is possibly significant that the organic materials so far found to exercise a "biological control" upon soil-borne fungus diseases, comprising green manures, animal manures, and cooked cereals and similar starch-containing supplements, are characterized by a nitrogen content either insufficient, or only just sufficient, for complete decomposition.

An exception to this possibly general experience is provided by the experiments of van der Poel (1938) on the control of bacterial slime disease (*Bacterium solanacearum*) of tobacco and tomato in Sumatra. This author obtained considerable reduction in the percentage of slime-diseased tomato plants grown in diseased soil by incorporation of green manures with the soil before planting. The best results were obtained, however, by the use of those green manures and other organic materials with the highest natural contents of nitrogen, such as groundnut meal, Kapok meal, and ground stalks of *Mimosa invisa*. The addition of supplementary nitrogen sufficient for complete decomposition of the organic material was found to result in a much greater reduction of slime disease in the tomato test plants. Thus ground leaves of *Macaranga* mixed with the soil resulted in a 12 per cent decrease of slime sickness, but when extra nitrogen was added, a decrease of 43 per cent in the disease was obtained. Ground leaves of *Imperata* gave a decrease of 16 per cent in slime-diseased tomatoes, but when extra nitrogen was added, the effect was a 46 per cent decrease in disease. These satisfactory results are attributed by van der Poel to biological control of *B. solanacearum*.

One of the results obtained by van der Poel—the failure to obtain appreciable disease reduction through addition of humus in the form of a black, highly organic soil—calls for further comment. A similar conclusion could also be drawn from the experiments of Garrett (1938a), in which a black fen soil of high organic content ("Downham") did not decompose the *Ophiobolus* mycelium so well as loam and clay soils of much lower organic content. It therefore appears that the value of organic matter for purposes of biological control may be directly related to its availability for decomposition ; upon reaching the stage of soil humus, it evidently becomes comparatively inert (Thom and Morrow, 1937).

This point is exceptionally well illustrated by some recent experiments of Goss (1937) on biological control of *Actinomyces scabies*. After demonstrating that the amount and severity of scab on his experimental potato tubers were directly related to the concentration of the pathogen in the soil, he proceeded to examine the effect of various soil treatments upon the development of scab, which was recorded as percentages of tubers falling into four or more different infection classes. In an experiment with a sterilized compost soil, of high organic content, inoculated with *A. scabies*, the greatest decrease in the amount of scab developing in the tubers was obtained by simultaneous addition to the soil of unsterilized manure, whilst the next greatest reduction followed the addition of a filtrate of the same unsterilized manure. A filtrate of unsterilized soil exerted a much smaller effect, evidently not hastening very appreciably the rate of recolonization by members of the general soil microflora, which was occurring in the sterilized but otherwise untreated control soil. Sterilized manure exerted, however, a controlling effect which was fully significant, though smaller than that of the unsterilized manure or its filtrate. This was tentatively attributed by Goss to the fact that the

additional organic matter increased the rate of recolonization by incoming micro-organisms. In a comparable experiment with an unsterilized field soil, however, the sterilized manure gave a much greater reduction of scab than the unsterilized manure, whilst a filtrate of unsterilized manure gave no reduction at all in scab, but actually an increase (of doubtful significance).

Table 3
(From the data of Goss, 1937)

		Infection classes of tubers determined by percentage of surface scabbed				No. of tubers in test
		0%	0-2%.	2-25%.	25-100%.	
Sterilized compost soil	No treatment	2	6	34	58	249
	Filtrate of unster. soil	8	17	27	48	176
	Filtrate of ster. manure	7	8	36	49	205
	Ster. manure	12	13	49	27	102
	Filtrate of unster. manure	20	22	34	24	215
	Unster. manure	54	17	23	6	78
Unster. field soil	No treatment	13	14	35	38	77
	Filtrate of unster. manure	12	4	30	54	30
	Unster. manure	39	20	20	21	99
	Ster. manure	55	24	16	5	147

These very interesting results may perhaps be interpreted as follows. In the sterilized compost, food material is high but initial numbers of organisms are low, so that the greatest development of microbiological activity (leading to biological control of *A. scabies*) follows the addition of unsterilized manure, high in numbers of micro-organisms, though lower in available energy material than the sterilized manure. In the unsterilized field soil, on the other hand, numbers of micro-organisms are relatively high but available energy material is very low, so that the greatest development of microbiological activity may here be expected to follow the addition of sterilized manure with the higher available energy content. In other words, the manure is most effective when it supplies what the soil chiefly lacks. At this point, it is interesting to recall earlier controversies as to how much of the fertilizing action of farmyard manure could be attributed to its content of micro-organisms, as an addition to the pre-existing soil population (Waksman, 1931, Russell, 1937).

The use of organic manure for the control of *Phymatotrichum omnivorum* root rot of irrigated cotton under continuous cultivation in Arizona has been established in a very striking manner by the experiments of King *et al.* (1934a). These authors supported their hypothesis of microbiological antagonism as the mechanism of control by an extensive study of the soil microflora in the treated and control plots by the Cholodny slide technique (Eaton and King, 1934), and by soil respiration determinations. They were able to demonstrate in this way that whereas the development of saprophytic organisms was most profuse in the slides buried in the manured plots, the mycelium of *P. omnivorum* was most abundant on the slides in the

unmanured plots. King (1937) has recently given precise directions for the control of *P. omnivorum* root rot in continuous cotton under irrigation in the Southwest U.S.A., by continued application of organic manures over a period of years. " The method consists of applications of various organic materials in deep furrows during the fall and winter, and in planting the cotton over the buried material. The furrows for the manure should be from 10-14 inches deep, so that the buried material will not interfere with the preparation of a seed-bed . . . It has been found that as much as 20 tons of horse or cow manure from corrals or open stalls per acre may be used without injury to the cotton crop. However 15 tons per acre probably would be adequate for most conditions. Where green material such as freshly cut alfalfa, clover, field peas, vetch or mustard is available, 30 tons per acre may be used if furrows are made deep enough so that the material may be covered with 5 or 6 inches of soil . . . Irrigation water should be applied immediately (i.e. after covering) so as to compact the soil and encourage the activity of organisms for decomposition. If possible, the organic material should be applied, covered, and irrigated at least a month before planting time, and a second irrigation should be made before planting to ensure adequate moisture for germination of the cotton seed."

In a long-term experiment conducted by King, a survey of the plots in 1935 showed that 1.6 per cent of cotton plants had died from root rot on 4 manured plots as compared with 56.2 per cent of plants killed by the fungus on the control plots. In another experiment, after only 2 years of the treatment, diseased plants occupied only 9 per cent of the area of the treated plots, as compared with an area of 50 per cent for the untreated control plots.

King's application of biological control has thus been directed, in part at least, towards inactivation of the pathogenic fungus in the soil *before the growing season of the crop*. It seems probable that only in this way will the biological method be used to its fullest advantage.

Another type of biological control has been reported by Weindling and Fawcett (1936), in experiments on checking damping-off of citrus seedlings by *Rhizoctonia solani* in California. Weindling (1932) had previously shown that the hyphae of *Rhizoctonia* are vigorously attacked and parasitized by the very common soil-inhabiting fungus *Trichoderma lignorum*. This parasitic action was found to be most effective under acid conditions, both in the soil and on culture media, for reasons partially, at least, elucidated by the further work of Weindling (1934) and of Weindling and Emerson (1936) (see also note by Weindling, 1937). There is probably a connection between these observations and the known predominance of *Trichoderma* in the more acid types of soil. In accordance with expectation from these studies on the hyperparasitism of *Trichoderma*, Weindling and Fawcett showed that the *Rhizoctonia* damping-off of citrus seedlings could be successfully controlled in laboratory, glasshouse and field experiments by acidifying the soil layers next to the seed by application of aluminium sulphate or acid peat moss, which produced a reaction of about

pH 4.0. Since damping-off by the *Rhizoctonia* still occurred in containers of sterilized acidified soil from which the *Trichoderma* had been effectively excluded, the effect of acidifying the unsterilized soil in controlling damping-off was attributed to the encouragement thus given to the *Trichoderma*.

Abundant inoculation of the unsterilized soil with *Trichoderma* spores at the time of acidification gave increased control of damping-off in some experiments ; in other experiments, the natural *Trichoderma* flora already present in the unsterilized soil was apparently sufficient to exert the maximum possible effect. Heavy inoculation with *Trichoderma* without acidification, however, proved completely ineffective—a further illustration of the axiom that *biological control must be ecologically produced, by furnishing the appropriate conditions for it to occur.* Weindling and Fawcett suggest that the sulphuric acid control of *Rhizoctonia* damping-off of conifer seedlings reported by Hartley (1921), Wiant (1929), and Jackson (1933) may be due to the action of *Trichoderma* spp. The experiments of Weindling and his collaborators have been confirmed by those of Bisby *et al.* (1933), Brown (1933), Allen and Haenseler (1935), Butler (1935) and Hino (1935) with the same fungus.

Biological control of the type investigated by Weindling, Garrett and others applies exclusively to the decomposition of vegetative fungus mycelium, whether actively growing or in a dormant condition in diseased plant residues. On the other hand, *Phymatotrichum omnivorum*, the subject of biological-control study by King and his collaborators, forms sclerotia, and the longevity of these in ordinary field soil is known to be very much greater than that of unorganized mycelium. Experiments will show in due course how susceptible fungus sclerotia of different species may be to decomposition by other soil micro-organisms, and whether their disappearance from the soil can be accelerated by methods of the type described above. A recent paper by Drechsler (1938) on the parasitism of the oospores of a number of Phycomycetes by two species—*Trinacrium subtile* and *Dactylella spermatophaga*—indicates that thick-walled resting spores possess no obvious resistance to this type of parasite. Chytridiaceous parasites of *Pythium* spp. had, however, been described at a much earlier date by Butler (1907). A good account of hyperparasitism of plant pathogenic fungi by other fungi is given in Weindling's (1938) review of this subject. We may therefore conclude that survival of the more resistant organs of plant pathogenic fungi, i.e. resting spores and sclerotia, is probably governed by the same laws of mortality as that of the vegetative mycelium.

It has been suggested that seedling blights caused by seed-borne pathogens may be susceptible of biological control, to some extent at least, and Christensen (1936) showed that barley seeds externally inoculated with *Helminthosporium sativum* gave a lower percentage of blighted seedlings in unsterilized than in sterilized soil. Naturally infected seed, however, carrying mycelium of *H. sativum* or *Fusarium* spp. internally gave as high a proportion of blighted seedlings in unsterilized as in sterilized soil. Henry

and Campbell (1938) report similar reduction in infection by two seed-borne parasites, *Polyspora lini* and *Colletotrichum lini*, of flax when the seed was planted in unsterilized v. sterilized soil. Contrary to the results of Christensen, they were forced to conclude that biological control by the soil microflora could act even upon internal seed infection, since appreciable infection of surface sterilized flax seed, which could only be due to internal infection, was found to occur in sterilized but not in unsterilized soil.

An interesting development in an analogous field is that reported by Linford *et al.* (1938), in the control of the root-knot nematode (*Heterodera marioni*) of pineapple by heavy applications of organic material. Chopped up pineapple plants were used as the organic supplement and cowpeas (*Vigna sinensis*) as the test plant for estimating the population of *H. marioni* in the soil after treatment. Additions of the organic material at the rate of 50, 100 and 150 tons per acre-foot of soil gave progressively greater reductions in number of galls, but 200 tons proved no more effective than the 150 tons dressing. When indicator plants were set in the treated soils after 1-5 months since the start of the treatment, the fewest galls developed after the shortest interval (one month), indicating that the population of *H. marioni* larvae was reduced early by the treatment, but later rose again. Linford *et al.* suggest that "decomposition results in a greatly increased population of total nematodes in the soil, and that these, in turn, support the building-up of large populations of plant and animal forms destructive to nematodes, including nema-capturing fungi, non-trapping fungal parasites, predacious nematodes, and predacious mites." This hypothesis is supported by reference to the work of Drechsler (1933-35) and others on fungi preying upon nematodes.

In conclusion must be described a quite different and entirely original method of biological control developed by Leach (1937) in Nyasaland. Whereas the previously described methods aim at the elimination of plant parasites either from infected plant residues or from the soil itself, the method of Leach is designed to replace the prospective parasite, *Armillaria mellea*, by harmless secondary parasites or saprophytes. After felling the jungle in preparation of a site for tea planting, there is vigorous and widespread infection of the roots of certain species, notably *Parinarium mobola*, by the fungus *Armillaria mellea*. This fungus occurs only to a moderate extent on the roots of the living jungle, but its development seems to be greatly facilitated by the lowered resistance of the roots after felling. *A. mellea* is then later on responsible for much trouble in the young tea plantations, which may suffer severely from its attack. The only control method previously known has been removal of the infected jungle roots and stumps from the soil. Leach has now found that if the jungle trees are ring-barked some time before felling, the roots are invaded not by *A. mellea*, but by certain other fungi, e.g. *Rhizoctonia bataticola* and *Botryodiplodia theobromae*, which are harmless in young tea plantations. He has attributed the failure of *A. mellea* to infect the roots of ring-barked

trees to its preference for roots with a normally high carbohydrate content, and considers that it may be unable to invade and parasitize those in which the carbohydrate content has been seriously depleted by ring-barking. Such a restriction might be due, of course, to the competition of other organisms better able to infect such roots low in carbohydrate content, rather than to absolute inability of *A. mellea* to colonize such a substrate.

(5) Adjustment of Soil Conditions to check Activity of the Parasite

Parasitic fungi may spread actively underground in three principal ways (Garrett, 1938b) :—

(i) Freely through the soil and over the underground organs of the host plant, e.g. *Rhizoctonia solani*, *Rosellinia* spp., and *Armillaria mellea*.

(ii) Along the outside of the host organs (which are immediately or subsequently invaded by the fungus), e.g. *Fomes lignosus*, *Phymatotrichum omnivorum* and *Ophiobolus graminis*.

(iii) Along the inside only of the host organs, e.g. *Fusarium oxysporum cubense* and other vascular *Fusaria*, and *Verticillium albo-atrum*.

The direct effect of soil conditions upon the fungus may be expected to diminish down the above series, in which the subterranean spread of the fungus becomes increasingly independent of the direct incidence of the soil environment, but at the same time more and more dependent upon host resistance as affected by soil conditions. Thus in the case of those fungi growing along the outside of the underground host organs, soil conditions may well determine whether an infection shall be slow of advance or even non-progressive, or whether it shall spread more or less rapidly in either direction. But with fungi in which underground spread is confined to the inside of the host organs, soil conditions can directly operate only on the actual process of infection, exerting merely an indirect influence upon the rate of spread inside the root, through modification of host physiology (e.g. *V. albo-atrum*, p. 42).

The underground spread of the less-specialized root-infecting fungi may be checked by their frequent inability to invade other than immature tissues of the host, with consequent localization of individual infections. The majority of the seedling blight pathogens, especially those causing damping-off, are limited in this way. If such fungi at the same time lack appreciable capacity for independent spread through the soil, their power of damaging the plant becomes correspondingly curtailed.

Certain special methods of controlling parasitic fungi have been based on their growth habit. Thus the spread of the tropical species of *Rosellinia* through the surface litter of fallen leaves in damp and shady situations, as described by Tunstall (1922), Nowell (1923) and Petch (1928), may be stopped by removing this litter, at least from around the stems of the plantation trees, and by taking every opportunity for ventilation and drying-out of the surface soil (Gadd, 1937).

One of the most important of the mechanical methods of disease control—that of rogueing—derives its efficacy from the fact that the majority of the more highly specialized root-infecting fungi cannot spread freely through the soil, but only along the outside or inside of the underground organs of the host, as indicated above. This restricts opportunity of spreading from one plant to another to bridges formed by root contacts. If, therefore, the diseased plant is removed together with the healthy ones surrounding it, it is often possible to eliminate the source of infection. The rogueing method may be combined with some form of soil disinfection before the same site is replanted, or the site may be left blank for a sufficient interval, if one is necessary. A difficulty inherent in the rogueing method is that by the time a plant is seen to be obviously diseased, adjacent plants have already become infected, and it may be found expedient to remove not only a first, but also a second ring of apparently healthy plants around the obviously diseased individual.

The history of attempts to control, by a rogueing method, the spread of Panama disease of bananas (or banana wilt) in Jamaica has been given by Cousins and Sutherland (1930), and by Smith (1932b). The disease was identified on the Island early in 1912, and discovery of two more outbreaks, in widely separated localities, shortly followed. These outbreaks, considered to be of independent origin, were attributed to plantation labourers returning from the diseased banana lands of Central America, and bringing back infected tools and planting material, in spite of strict watch for such practices on the part of customs officers and plant quarantine inspectors. The Jamaican Department of Agriculture suspected from the first that Panama disease spread along the roots of the banana plants rather than directly through the soil, and from one plant to another by root contact. Cousins and Sutherland very aptly described this mode of spread as " chain action." A drastic Quarantine Regulation was therefore drafted in 1912, whereby all plants within one chain radius of the original diseased plant had to be removed and destroyed, making a quarantine area of four square chains around the site of each diseased plant ; the quarantine area was not to be replanted with bananas. The selection of a one-chain (22 yards) radius was based on the finding that the longest roots of a banana plant did not extend for a radius of more than half a chain (11 yards). In proof of the correctness of the original assumption that the disease spread by " chain action " along the roots of the plants, Cousins and Sutherland cite as example plots rogued by this method in 1915, where in 1930 healthy bananas still surrounded the original quarantined areas. This was considered to disprove the assertion that the causal fungus, *Fusarium oxysporum cubense*, could travel independently through the soil in the absence of the banana plant. The loss of all the healthy plants on an area of 4 square chains was a heavy one to the planters, in spite of compensation, and with increase in the incidence of the disease in any locality, a compromise was eventually made between economic considerations and the requirements of the rogueing treatment. Under a

Panama Disease Order of 1925, a graded reduction in the quarantine area was permitted, as follows. For the first three cases on any property, an area of 4 square chains was to be enforced, for the fourth and fifth cases, one square chain, and after the fifth case, an area of half a square chain was to be quarantined. Thereafter, with approval of the Director of Agriculture, the quarantine area might be reduced to the " nine root system," whereby only the eight healthy plants surrounding each diseased one had to be removed and destroyed. Cousins and Sutherland state that experience had shown the rate of spread of the disease to increase with each relaxation of the quarantine restriction. Smith (1932b) confirms this conclusion, and remarks that up till 1932 the quarantine regulations had met with success at least in checking the rate of spread of Panama disease. The " one root system," whereby the diseased plant alone was removed and destroyed, was to be deprecated as very dangerous, and permissible only when the property was officially gazetted as infected, and adjacent lands were not endangered.

Unfortunately for the strenuous and well-directed efforts of the Jamaican Department of Agriculture, however, rogueing could prevent only the active spread of the wilt fungus, and could not stop other modes of dispersal. From the beginning, according to Smith (1932b), the effectiveness of the quarantine operations was vitiated by non-cooperation on the part of some of the planters, more particularly small-holders, who not only failed to report infections, but carried out the unauthorized one-root treatment on their own. In efforts to discover a " cure " for the disease, certain individual planters carried out all sorts of secret experiments on their own land, generally without taking proper precautions against the spread of infection. Diseased material was sometimes burnt, but might even be thrown into an adjacent stream, to avoid detection! Small settlers, again, had been known to plant up a new area with diseased banana suckers obtained from adventitious growth on quarantined land. One of the most effective agencies for passive spread of *Fusarium oxysporum cubense* has been that of flood and river water. Smith considers that dissemination of the fungus by surface wash from local flooding after heavy rains is particularly important ; another dangerous practice is that of planting bananas right up to the banks of rivers bordering plantations. Finally, after commenting upon the loss to banana cultivation of large areas of the best alluvial soils in the river valleys and level lands, due to flood dispersal of the disease, Smith (1936) reports the decision of the Department of Agriculture, taken in 1935, to permit one-root treatment of the disease throughout the Island. The future of the banana industry in Jamaica now probably depends upon the disease-resistant selections at present under improvement by the Agricultural Department.

The use of rogueing methods in the control of root diseases of rubber in Malaya has already been described (p. 22). Rogueing methods have been developed chiefly in response to the need for some method of checking the spread of root disease in plantation crops, and are not likely to find

favour with growers of annual field crops. McKay (1926), however, has published an interesting study of attempted control of the *Verticillium albo-atrum* wilt of potatoes by the " three plant method " of rogueing, whereby a visibly wilted plant was pulled together with its two immediate neighbours in the row. Infection by root contact appeared to spread much more rapidly along than across rows ; this was attributed by McKay not so much to the greater distance apart of plants between than along rows, as to the fact that root development and root contact between the rows had been checked by frequent cultivations during the earlier part of the growing season.

A quite different method of checking the underground spread of a root-parasitic fungus, but one which also depends upon root-contact spread, has been developed by Taubenhaus and Ezekiel (1931) for the control of *Phymatotrichum omnivorum*. The method consists in the isolation of diseased from healthy areas by root barriers formed by four rows or more of sorghum plants (resistant to *P. omnivorum*). The sorghum root barriers break the continuity of root-contact between adjacent areas of cotton. This method, like that of biological control, really represents a partial return from the highly artificial methods of crop cultivation to a system less remote from the natural mixed association of plants. It is likely that the future may see a further development of this type of control method.

Turning now to more general methods of preventing spread of root-infecting fungi, there is, of course, the oldest-established mechanical method of trenching. This method was evolved in the days when the majority of these fungi were supposed to be able to spread freely through the soil, and so trenching was the most obvious method of stopping such spread. With increase in knowledge of the growth habits of the pathogenic fungi, the method of rogueing has come into more general favour, and trenching is less used.

One of the difficulties in effective control by trenching is that the trenches require maintenance in proper condition by periodical inspection and cleaning out. Another difficulty also occurs, to obviate which a new method of trench management has recently been devised by Napper (1937), to meet the needs of disease control in mature rubber areas. The fungi concerned are *Fomes lignosus*, *F. noxius*, and *Ganoderma pseudo-ferreum*. Trenching may have been decided upon as a temporary expedient for stopping the spread of these organisms along the roots of the mature stand. (The only permanent method of disease eradication in an old stand is by thorough digging-through of the diseased patches with removal of infected roots—to be followed by routine rogueing of the new young stand replacing it, as described on p. 22.) Having made sure, by the examination of roots cut through during the trenching process, that the trench passes well outside the diseased area, the trench is then filled up again to a depth of not less than 18 inches from the floor, efficiency being restored by redigging every 18 months or two years. If the trench is

left permanently open, the roots of the trees eventually find their way under its floor, so that it becomes necessary progressively to deepen permanently open trenches. The refilled trench, on the other hand, becomes full of small roots in six months, but infection passes through these only very slowly (p. 21).

A variant of the open-trench method has been employed in Texas (Taubenhaus and Ezekiel, 1931), and in Arizona (Streets, 1937), by the use of trenches filled with mixtures of soil and heavy oils, sulphur, ammonia, carbolic acid or salt, for stopping the spread of *Phymatotrichum omnivorum*.

It finally becomes necessary to consider the large group of control methods based upon the adjustment of soil conditions in such a way as to reduce the amount of disease developing in the crop. Although the effect of soil conditions in reducing the amount of disease in the crop does not necessarily operate by direct action upon the parasite, it has been considered to do so in the case of a large number of soil-borne fungus diseases. Some degree of natural control by soil conditions can generally be discovered by a preliminary survey of the incidence of a soil-borne disease on different soil types, and under different systems of cultivation. Further research work on the mechanism of the effect not infrequently results in the evolution of a useful control measure.

The commoner soil-borne fungus diseases of economic plants have already been grouped elsewhere (Garrett, 1938b) according to their behaviour with respect to soil moisture, texture, organic matter, reaction and chemical composition. It is therefore proposed here only to quote some instances of important diseases which can be controlled by adjustment of soil conditions in such a way as to hinder the underground activity of the parasite during the growing season of the crop.

The effect of soil temperature upon disease is best considered in the next Section (6), since temperature appears to operate chiefly by modifying host reaction to infection, often in a very striking manner. Rising soil temperature exerts, at the same time, a direct effect upon the fungus, generally by increasing its rate of growth and metabolism; thus the optimum temperature for growth upon agar media is in the neighbourhood of 25°C. for most of the root-infecting fungi (Jones *et al.*, 1926). Lower optimum temperatures are found in a few parasitic soil fungi, such as *Plenodomus meliloti*, which was found by Sanford (1933b) to grow best at 15°-17° C. This organism is responsible for brown root rot of sweet clover in Alberta, and is chiefly active during the thawing-out of the frozen soil in early spring. Soil temperature can also act indirectly upon a parasite in another way, namely, by increasing the rate of its inactivation or decomposition by the other soil micro-organisms (Henry, 1932; Garrett, 1934), so that the influence of this factor upon the prevalence of a soil-borne disease is a complex one.

Soil moisture exerts a direct effect upon the activity of certain fungi, especially those belonging to the Phycomycetes and other lower groups. With these organisms, infection is generally brought about by free-swim-

ming zoospores, which require a film of water of adequate thickness for germination and penetration of the host root. Occurrence of infection is thus frequently limited to conditions of high soil moisture content, and may take place only after heavy rainfall, or on the more low-lying parts of a field, when attention to drainage may be found helpful. Examples of such diseases are club-root of crucifers, due to *Plasmodiophora brassicae* (Monteith, 1924), root rot of peas caused by *Aphanomyces euteiches* (Haenseler, 1926), root rot of sugar cane (Carpenter, 1934) and of corn (Johann *et al.*, 1928) caused by *Pythium arrhenomanes*, crown rot of rhubarb due to *Phytophthora cactorum* (Beach, 1922), pineapple wilt due to *P. cinnamomi* (Lewcock, 1935) and damping-off of seedlings caused by *P. parasitica* and *P. cryptogea* (Bewley, 1923).

Soil texture and aeration have a particularly pronounced effect on the activity of the root-infecting fungi. It is true that certain weak parasites can only infect the host when it is injured by waterlogging or other cause of deficient soil aeration (p. 43). But, apart from this, the activity of pathogenic fungi seems generally to be favoured by soils of light texture and good aeration. Waksman (1931) states that saprophytic fungi are most active in the decomposition of plant residues under conditions of abundant soil aeration. Examples of important soil-borne diseases favoured by good soil aeration are potato scab (*Actinomyces scabies*), take-all of wheat (*Ophiobolus graminis*), and Panama disease of bananas (*Fusarium oxysporum cubense*). Potato scab is generally reported as worst on soils of light texture and medium to low moisture content, and therefore most prevalent in dry years (Millard, 1923, Sanford, 1923, Dippenaar, 1933), though there are inconsistencies in its occurrence which have been recently discussed by Goss (1937). *Ophiobolus graminis* is especially sensitive to soil aeration (Garrett 1936-37); the importance of a well-compacted soil for control of the take-all disease of wheat has been appreciated in South Australia for some 60 years, and Griffiths (1933) gives an interesting account of the way in which all cultivation operations on the wheat fallow are directed towards the consolidation of the seed-bed. Reinking (1935) has shown that banana wilt is serious only on light-textured soils, and that this restriction is to be correlated with numbers of the causal organism in the soil. Control of this disease is now being sought in a new way, not by soil management, but by restriction of new plantings to the heavier soils naturally unfavourable to the development of Panama disease.

The influence of soil reaction upon soil-borne diseases is often very striking, and the preference of club root of crucifers for acid soils and of potato scab for alkaline soils has been known for a long time (Halsted, 1900). Some important diseases recently added to the list of those favoured by alkaline soils are *P. omnivorum* root rot of cotton (Taubenhaus *et al.*, 1937), *Thielaviopsis basicola* black root rot of tobacco (Morgan and Anderson, 1927, Doran, 1931), and take-all of wheat (Garrett, 1936-37). Control of such diseases by modification of soil reaction alone is not

generally a practical possibility, owing to the difficulty of changing sufficiently the reaction of the more highly buffered soils, and to the usual preference of the crop plant itself for a soil not too far removed from neutrality. As an adjunct to other methods of plant protection, however, increasing use will probably be made of soil reaction control.

The role of soil organic matter and the function of green manuring have already been discussed in connection both with biological control of the more specialized parasites, and with the converse behaviour of fungi of the *Rosellinia* type ; further reference to organic matter here is therefore unnecessary.

(6) Augmentation of Host Resistance

There is a large class of soil-borne diseases of plants in which the pathological condition may be closely associated with a particular fungus, but yet due in the ultimate analysis to some injurious non-biological condition of the environment. In other cases, no single organism is alone constantly associated with the diseased condition, but a complex of fungi and other micro-organisms, the individual parasitic capabilities of which may, indeed, be comparatively slight. Examples of such troubles are root rot of cotton in the Sudan (Massey, 1935-36, Andrews and Clouston, 1938), germination injury of peas in England (Hull, 1937), and root rot of strawberries (Hildebrand, 1934) and raspberries (Berkeley, 1936) in Canada. From a general survey of plant-disease literature, Jarvis (1932) concluded that the further the cultivation environment is removed from the natural " ecological optimum " of a crop plant, the more liable is the crop to diseases of this type.

At the same time, there are a considerable number of parasitic diseases which cannot be directly or indirectly attributed to any unfavourable condition of the non-biological environment, but which can be controlled by environmental modification of host resistance to the fungus. Examples of this are most common where temperature relations are concerned ; in the absence of the parasite, healthy plants may be raised under a comparatively wide range of temperature conditions, but where it is present in the soil, the temperature range for healthy growth of the plant becomes restricted accordingly.

The temperature relations of a number of important crop plants and their chief soil-borne diseases have been exhaustively studied by means of a controlled environment technique worked out at Wisconsin. A full account of this work is given by Jones *et al.* (1926). Diseases found to be favoured by high soil temperature were cabbage yellows (*Fusarium conglutinans*), flax wilt (*F. lini*) and tomato wilt (*F. bulbigenum* var. *lycopersici*) ; other diseases were found to be promoted by low soil temperature, viz, onion smut (*Urocystis cepulae*), tobacco root rot (*Thielaviopsis basicola*) and potato stem canker (*Corticium solani*). The seedling blights of wheat and maize, studied by Dickson (1923), show a particularly interesting relation to temperature. The pathogenic organism, *Gibberella saubinetii*,

is the same in each case, but maize is affected chiefly at low soil temperatures (8°-16° C.), and wheat at high soil temperatures (16°-28°C.). The optimum temperature for seedling blight of each cereal is therefore that furthest removed from the optimum soil temperature for the development of the underground parts of the host plant. The biochemical reasons for the development of resistance to the seedling-blight organism at the optimum temperature for normal maturation of the developing tissues of these two cereals have been elucidated by the further work of Dickson *et al.* (1923), and of Dickson and Holbert (1926). The studies of these different workers upon the temperature relations of soil-borne diseases in the Wisconsin temperature tanks have been correlated by Jones *et al.* (1926) with the distribution of the respective diseases according to latitude in the U.S.A. Thus whereas onion smut, a low-temperature disease, does not occur in the southern states of the U.S.A., cabbage yellows, with a high optimum temperature, is not found in the northern parts of the northern states. In the same way, the appearance of a soil-borne disease in different years, and at different seasons of the year, may be similarly determined by soil temperature.

Control of a soil-borne disease by means of its temperature relations in the field is more or less confined to variation in the date of sowing, and this method of control is effective chiefly with diseases, such as onion smut and bunt of wheat, in which infection occurs in the seedling stage or not at all. Control of soil temperature in the glasshouse, however, is more easily accomplished, and forms the basis of a valuable control method for the *Verticillium albo-atrum* wilt of the tomato discovered by Bewley (1922). This disease is of importance in English glasshouses chiefly in the early summer and again in the autumn months, and is rarely found in the latter half of June, July or August. Bewley found that, whilst the optimum temperature for the development of the disease was 21°-23°C., temperatures above 25°C. exerted a striking control, not only preventing the occurrence of the wilt, but actually bringing about the recovery of already wilted plants. The controlling effect of high temperature was found to be enhanced by suitable shading of the plants. Bewley (1923) gives the following directions for control of the disease in this way (p. 82): "As soon as the wilt appears and it is proved that *Verticillium albo-atrum* is the pathogen, the average temperature of the houses should be raised above 25°C. by suitably increasing the boiler heat, regulating the ventilation, and by closing down the houses from two to four hours in the middle of the day. A light dressing of whitewash on the glass makes the conditions still more favourable for the plants. As little water as possible should be given to the roots, as heavy watering merely aggravates the wilting, but a light overhead damping helps the wilted plants to recover. The plants should be encouraged to make fresh roots above the original diseased ones by placing fresh soil round the base of the plant." Bewley records that in one nursery where these control measures were carried out, the percentage of wilted plants was reduced from 68 to 10 in a fortnight.

Different phases of the same disease may have quite distinct temperature optima. For example, Porter and Melhus (1932) found that whereas pre-emergence rot of water-melon seedlings due to *Fusarium bulbigenum* var. *niveum* was more severe at a low temperature (16°-18°C.) than at a high temperature (25°-28°C.), the wilting of the young seedlings was more serious at the higher temperature. An almost identical observation has been made by Greeves and Muskett (1936), who found that whereas pre-emergence killing of swede seedlings was greatest at the lowest temperature (6°C.) in their experiment, the damping-off of the emerged seedlings was greatest at the highest temperature (23°C.). Both pairs of investigators attribute the high incidence of pre-emergence killing at low temperatures to delayed emergence of the seedlings.

Several diseases are closely associated with defective soil aeration due to waterlogging or other cause. Violet root rot of tea, due to *Sphaerostilbe repens*, is stated by Tunstall (1922) to be confined to waterlogged and acid soils ; even badly affected bushes were found to recover after appropriate soil treatment, i.e. drainage and liming. Stiff soils are especially favourable to the occurrence of this disease. Walters (1935) found the same fungus causing red root of limes in St. Lucia only in poorly-drained orchards where root damage from periodical floods was evident ; the fungus was stated to be present, but non-parasitic in the soil of the drier orchards. Root rot or wilt of cotton in the Sudan, the immediate cause of which is an attack of the finer rootlets and distal ends of the laterals by a complex of soil fungi, is reported by Massey (1935-36) to be associated with years of high rainfall and soils of high alkali content. There are difficulties, however, in attributing the trouble solely to poor root aeration in these exceptionally heavy and alkaline soils (Andrews and Clouston, 1938). Factors predisposing sugarcane to *Pythium arrhenomanes* root rot under the conditions of high water table and impeded drainage in the heavy clay soils of the Louisiana sugar belt have been investigated by Rands and Dopp (1938). Hydrogen sulphide and salicylic aldehyde were selected as examples of substances accumulating in soils under semi-anaerobic conditions, and the effect of these two substances upon the predisposition of sugar cane to *Pythium* root rot in nutrient sand culture was tested. Hydrogen sulphide was not found significantly to intensify the effects of the disease. On the other hand, salicylic aldehyde in concentrations of 20 to 40 p.p.m., which had little if any influence on cane growth in the absence of the fungus and showed no effect on the growth of the fungus in culture, apparently so predisposed the roots to infection in the presence of the fungus as to result in a reduction in weight of the plants from 2 to 7 times as great as that caused by the presence of the fungus alone.

Too heavy demands on the yielding capacity of the crop plant may also result in the appearance of disease. " Internal root rot " of tea, formerly attributed to *Botryodiplodia theobromae*, was shown by Gadd (1928-29) to be due in Ceylon to cultural practices. This " disease " occurs in Ceylon chiefly at middle and low elevations, where the plucking

rounds are most frequent, and the pruning cycle the shortest ; it is manifested as a failure to make fresh growth after pruning, and by subsequent death of the bush. Gadd showed that failure to recover after pruning appeared to be invariably associated with absence of starch reserves in the roots, and that this condition actually *preceded* infection by *Botryodiplodia*. Lack of starch reserves thus appeared to be the cause, and the general subsequent infection of the weakened roots by *Botryodiplodia* merely an effect of the disease. In tea grown at the higher elevations, where assimilation could better keep pace with growth, the disease was almost unknown. Gadd also observed that whereas roots infected by *Botryodiplodia* were completely deficient of reserve starch, those infected by *Poria, Rosellinia* and *Ustulina* showed a normal starch content (cf. Leach (1937), p. 34 above). Carpenter (1936) has observed that the death of tea bushes due to excessive reduction in leaf area as a result of overplucking or premature defoliation is associated in N. India with *Botryodiplodia theobromae* on light sandy soils, but with *Sphaerostilbe repens* on the stiff heavy soils.

The diseases associated with manurial deficiencies or lack of balance may lastly be considered. It is not proposed to treat here of the variety of pathological conditions proved to be due solely to lack of one or other of the so-called minor elements for plant nutrition, as these have already been reviewed in Technical Communication No. 31. The three major elements essential for plant nutrition are nitrogen, phosphorus and potash ; deficiency in any one of these, or a lack of proper balance between them, may weaken the plant and predispose it to fungus infection. Thus browning root rot of cereals due to *Pythium arrhenomanes* in Canada (Vanterpool *et al.*, 1930-35) and root rot of sugar cane in Hawaii (Carpenter, 1934), caused apparently by the same species (Drechsler, 1936), are both reported to be associated with a low phosphate and high nitrate status of the soil. In soils of higher phosphate-nitrogen ratio, infection by the *Pythium* is still sufficiently abundant, but the damage to the host plant is very much less. The results of Vanterpool so far published suggest that the resistance of wheat to browning root rot in soils of higher phosphorus content is due less to any demonstrable increase in resistance to infection of individual roots than to an increase in rooting capacity of the wheat plant under conditions of better phosphate nutrition. The remarkable power possessed by the wheat plant, when growing under good conditions, of putting out fresh secondary roots to replace those lost by disease has been ingeniously demonstrated by the root-cutting studies of Simmonds and Sallans (1930-33). The browning root rot disease is stated by Vanterpool to be worse in crops after fallow than in those sown on stubble land—in contrast to experience with other cereal root rots. This is attributed by Vanterpool to increase in the available nitrogen content of the soil after fallowing, as a result of the accumulation of nitrate. A possibly analogous case has been reported by Grandfield *et al.* (1935), who found in Kansas that stands of alfalfa seedlings were progressively decreased through damping-off by *Pythium* spp. with increase in the preceding period of fallow from 2-5 years.

Thus only 33 per cent of the original stand of alfalfa seedlings survived till the following spring on the five years' fallow plot, as compared with a survival of 70 per cent on a plot under rotation of sorghum, corn, wheat, oats and alfalfa. Under the dry-land farming conditions in Kansas and Saskatchewan, it is necessary to store up soil moisture by a year's fallow in order to get a good crop of wheat, or successful establishment of alfalfa.

The effect of superphosphate in reducing the loss due to the take-all disease of wheat is well known in South Australia, and is demonstrated by field data collected by Samuel (1934). Such response in disease control has followed, however, on soils deficient in phosphate, and giving a good yield response to this fertilizer. A positive response in yield to superphosphate was obtained by McRae and Shaw (1933) on the permanent manurial plots at Pusa under a rotation of pigeon-pea with maize and oats—yet this fertilizer consistently increased the incidence of pigeon-pea wilt due to *Fusarium vasinfectum*, whilst green manuring as consistently reduced it.

Whilst the *Pythium* root rots of sugar cane and cereals are aggravated by application of nitrogen, root rot of peas due to another phycomycetous fungus, *Aphanomyces euteiches*, was reported by Martin (1934) to be reduced by nitrogenous fertilizers in New Jersey. Successful control of this pea root rot by nitrogen in pot tests and in small field plots was also obtained by Geach (1936) in Australia. The growth of *A. euteiches* on agar media was found by Geach to be especially sensitive to the nitrogen content of the medium. Thus on cornmeal agar with 2 per cent of peptone, formation of oogonia and antheridia by the fungus was suppressed, and the mycelium alone was no longer culturable after 33 days at laboratory temperature. On cornmeal agar without peptone, however, oospores were formed, and these remained viable over the period tested (60 days). Further evidence is needed, however, to bridge the rather wide gap between the observed behaviour of *A. euteiches* in pure culture on the agar plate, and the reaction of the disease to the application of nitrogenous fertilizers to the soil.

Deficiency of nitrate nitrogen was considered by Clayton (1923) to explain the resistance of tomato plants grown in saturated soil to wilt (*Fusarium bulbigenum* var. *lycopersici*). Inoculation experiments in nutrient sand culture with and without nitrate appeared to support his conclusion, and Fisher (1935) also reported that deficiency of nitrogen inhibited infection in sand culture experiments. Methods of estimating infection employed by Clayton and by Fisher have been criticized by W. S. Cook (1937) in the light of his own recent experiments. Cook showed that the *Fusarium* could be recovered by culturing from stem tissues not showing any vascular browning, or other macroscopic disease symptom. Using this improved method for detection of the fungus, Cook found that a high percentage of infection occurred in the minus nitrate cultures, but that the nitrogen deficiency tended to inhibit expression of symptoms. Nitrogen deficiency did not, therefore, inhibit infection, but did increase the resistance of the plant to the effects of infection in the post-invasion stage.

Applications of potash fertilizers are well known to reduce infection of the leaves and other aerial parts of plants by such parasites as the rusts and mildews. The effect of potash on a soil-borne infection has been extensively studied by Young (1938) for cotton wilt (*Fusarium vasinfectum*), in a 9-years' series of field experiments carried out at 15 different centres in Arkansas. Field observations at an earlier date had indicated a correlation between incidence of " rust," correctly attributed by Atkinson (1892) to potash hunger, and that of the *Fusarium* wilt. Young found that fertilizers containing potash gave control of rust and at the same time reduced wilt in every year and every location, except two. Increasing applications of potash gave, up to a point, increased control of the wilt. Whilst nitrate alone had little or no effect on the incidence of wilt, the application of acid phosphate and nitrate together appeared to aggravate both rust and wilt ; where acid phosphate was used alone, the effect was still more pronounced.

These investigations thus confirm the findings of plant physiology, that for healthy growth the plant not only requires a sufficiency of the three major elements, N P K, but must also be presented with these elements in some sort of balance. In conclusion, some reference is required to the experiments of Millikan (1938) in Victoria, who found that applications of zinc sulphate at rates of 15 and 30 lb. per acre considerably improved the growth of wheat crops suffering from a combined attack of eelworm (*Heterodera schachtii*) and of a number of root-rot fungi, namely, *Helminthosporium sativum, Curvularia ramosa, Fusarium culmorum, Rhizoctonia solani,* and others. The treatment did not apparently give any appreciable reduction in the number of roots infected by the parasites, but, by greatly increasing the rooting capacity of the plant, minimized the damage due to such infection. The action of zinc sulphate on the Victorian eelworm and root-rot attack thus seems, superficially at least, to resemble that of superphosphate upon the browning root rot of cereals in Canada.

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